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PROCEEDINGS
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FIRST APPROXIMATION OF PRESSURE DISTRIBUTION ON CURVED PROFILES AT SUPERSONIC SPEEDS

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Communicated September 14, 1949

1. Introduction.—In a paper[1] recently written we considered the problem of pressure distribution on curved profiles in a field of uniform supersonic gas flow under the assumption that a shock wave originated at the vertex of the obstacle. Behind the shock the flow was assumed non-isentropic and rotational, although viscosity and thermal conductivity were neglected. The pressure p was represented by a function $p(\omega, S)$ where ω denotes the inclination of the stream lines and S the entropy. Choosing the arbitrary constant in the entropy function so that $S = 0$ along the profile the required pressure distribution is given by $\theta(\omega) = p(\omega, 0)$ in which ω is the inclination at points of the profile. A formal solution of the flow problem is obtained which satisfies the boundary and shock conditions, provided that the function $\theta(\omega)$ satisfies an ordinary differential equation of infinite order. This differential equation appears in the form of a power series with coefficients which are functions of the inclination ω of the profile; moreover the coefficients, after the first, involve derivatives of the function $\theta(\omega)$. When this power series is terminated after the sum of its first n terms, we obtain an equation for the nth approximation of pressure on the boundary.

It is the purpose of this paper[2] to treat the determination of pressure by means of the first approximation which is given by

$$\frac{\theta}{p_1} = \frac{2\gamma}{\gamma + 1}(M^2 \sin^2 \alpha - 1) + 1, \tag{1}$$

where M is the Mach Number of the uniform flow before the shock, p_1 its

pressure, and the inclination ω of the profile is related to the parameter α in (1) by the equation

$$\tan \omega = \frac{2[(M^2 - 1) \tan^2 \alpha - 1]}{[(\gamma - 1)M^2 + 2] \tan^3 \alpha + [(\gamma + 1)M^2 + 2] \tan \alpha} \quad (2)$$

We take the constant γ to have the usual value 1.405. *The pressure given by this approximation at a point of the profile at which the inclination is ω is the same as that immediately behind the shock line at the point where ω gives the inclination of the stream line.*

2. *Computations and Graphs.*—Consider the profile formed by two circular arcs of radius $r = 150$ and chord length 60 as shown in figure 1. We shall calculate the pressure distribution on the upper contour of this profile for various values of the angle of attack a when the incident flow has Mach Number $M = 2.13$. This particular profile and Mach Number are selected, since these have been used by A. Ferri[3] in connection with his pressure determinations at the high-speed tunnel at Guidonia. Thus we shall be in a position to compare our calculated values of pressure with experimental determinations.

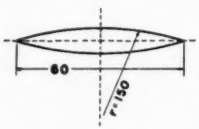

FIGURE 1

Table 1 shows the relation between α and ω computed in accordance with equation (2) for values of α ranging between 10.2667 (for which θ/p_1 vanishes) and 65, inclusive. By interpolation from this table, we can find the value of α corresponding to any point of the profile at which ω is known and hence by means of (1) we can find the value of the pressure ratio θ/p_1 at this point. At the per cent chord of the profile having the value β it is easily seen that the value of ω is given by

$$\sin \omega = 0.2 - \beta/250.$$

Using this relation, we can find the value of ω at the per cent chord β and hence the values of α and θ/p_1 as above stated.

In tabulating his results Ferri has referred the values of the pressure along the profile to the value of the pressure before the shock, and for purposes of comparison we shall adopt the same procedure. Thus, instead of the ratio θ/p_1 we shall list the values of the ratio

$$P = \frac{\theta - p_1}{p_1}.$$

At a point of the profile at which the pressure is greater than p_1 the value of P will be positive and the value of P will be negative whenever the pressure is less than the pressure in front of the shock.

The results of these calculations are entered in tables 2 to 11. Each

table corresponds to a different angle of attack a which is given at the top of the table. Also the experimental value of the pressure p_1 is shown at

TABLE 1

α(DEG.)	ω(DEG.)	θ/p_1	P	α(DEG.)	ω(DEG.)	θ/p_1	P
10.2667	−36.8330	0.0000	−1.0000	38	11.0110	1.8411	0.8411
11	−34.3208	0.0245	−0.9755	39	11.9278	1.9307	0.9307
12	−31.1333	0.0606	−0.9394	40	12.8167	2.0219	1.0219
13	−28.1875	0.0999	−0.9001	41	13.6777	2.1136	1.1136
14	−25.4500	0.1417	−0.8583	42	14.5167	2.2049	1.2049
15	−22.9000	0.1868	−0.8132	43	15.3167	2.2970	1.2970
16	−20.5112	0.2345	−0.7655	44	16.1042	2.3898	1.3898
17	−18.2612	0.2848	−0.7152	45	16.8500	2.4821	1.4821
18	−16.1500	0.3379	−0.6621	46	17.5777	2.5743	1.5743
19	−14.1722	0.3935	−0.6065	47	18.2722	2.6671	1.6671
20	−12.2778	0.4518	−0.5482	48	18.9417	2.7588	1.7588
21	−10.4833	0.5128	−0.4872	49	19.5792	2.8510	1.8510
22	− 8.7888	0.5753	−0.4247	50	20.1888	2.9422	1.9422
23	− 7.1612	0.6405	−0.3595	51	20.7722	3.0328	2.0328
24	− 5.6083	0.7084	−0.2916	52	21.3167	3.1230	2.1230
25	− 4.1222	0.7784	−0.2216	53	21.8333	3.2125	2.2125
26	− 2.6888	0.8504	−0.1496	54	22.3167	3.3010	2.3010
27	− 1.3222	0.9242	−0.0758	55	22.7625	3.3890	2.3890
28	− 0.0000	0.9999	−0.0001	56	23.1750	3.4744	2.4744
29	1.2722	1.0773	0.0773	57	23.5500	3.5603	2.5603
30	2.5000	1.1568	0.1568	58	23.8888	3.6435	2.6435
31	3.6888	1.2374	0.2374	59	24.1833	3.7267	2.7267
32	4.8388	1.3201	0.3201	60	24.4375	3.8073	2.8073
33	5.9500	1.4038	0.4038	61	24.6458	3.8863	2.8863
34	7.0278	1.4892	0.4892	62	24.8055	3.9636	2.9636
35	8.0667	1.5756	0.5756	63	24.9167	4.0399	3.0399
36	9.0778	1.6631	0.6631	64	24.9750	4.1137	3.1137
37	10.0612	1.7516	0.7516	65	24.9792	4.1858	3.1858

TABLE 2

$a = 0$; $p_1 = 52.1$; $q = 165.5$

% CHORD	ω(DEG.)	α(DEG.)	CAL. P	EXP. P	CAL. Q	EXP. Q
0.0	11.5388	38.5757	0.8927	....	4.2014	....
4.0	10.6000	37.5673	0.8024	0.8253	3.7764	3.8973
12.5	8.6278	35.5549	0.6242	0.5566	2.9377	2.6284
21.5	6.5445	33.5516	0.4509	0.3839	2.1221	1.8127
31.0	4.3612	31.5847	0.2858	0.2399	1.3451	1.1329
40.5	2.1778	29.7376	0.1359	0.0960	0.6396	0.4532
50.5	− 0.1167	27.9117	−0.0068	−0.0289	−0.0320	−0.1360
59.0	− 2.0612	26.4592	−0.1157	−0.1440	−0.5445	−0.6798
68.5	− 4.2445	24.9177	−0.2274	−0.2591	−1.0702	−1.2236
78.5	− 6.5945	23.3649	−0.3347	−0.3551	−1.5752	−1.6767
87.5	− 8.6722	22.0716	−0.4200	−0.2975	−1.9767	−1.4048
97.0	−10.8333	20.8050	−0.4991	−0.2975	−2.3490	−1.4048

TABLE 3

$a = -2$; $p_1 = 52.2$; $q = 166$

% CHORD	ω(DEG.)	α(DEG.)	CAL. P	EXP. P	CAL. Q	EXP. Q
0.0	13.5388	40.8387	1.0988	....	5.1714	....
4.0	12.6000	39.7562	0.9997	0.9962	4.7050	4.6988
12.5	10.6278	37.5965	0.8050	0.7471	3.7887	3.5241
21.5	8.5445	35.4726	0.6170	0.7184*	2.9038	3.3886*
31.0	6.3612	33.3815	0.4364	0.4215	2.0539	1.9880
40.5	4.1778	31.4252	0.2726	0.2874	1.2830	1.3554
50.5	1.8333	29.5611	0.1219	0.2107	0.5737	0.9940
59.0	−0.0612	27.9537	−0.0036	0.0575	−0.0169	0.2711
68.5	−2.2445	26.3251	−0.1256	0.0000	−0.5911	0.0000
78.5	−4.5945	24.6822	−0.2438	−0.0766	−1.1474	−0.3614
87.5	−6.6722	23.3149	−0.3381	−0.1628	−1.5912	−0.7681
97.0	−8.8333	21.9737	−0.4265	−0.1916	−2.0073	−0.9036

* The figure in the table of experimental results given by Ferri, from which these values are derived, appears to be a misprint. We have therefore not indicated the corresponding experimental point on the graph in figure 3.

TABLE 4

$a = +4$; $p_1 = 52.3$; $q = 166.5$

% CHORD	ω(DEG.)	α(DEG.)	CAL. P	EXP. P	CAL. Q	EXP. Q
0.0	7.5388	34.4919	0.5317	....	2.5024	....
4.0	6.6000	33.6031	0.4553	0.4685	2.1428	2.2072
12.5	4.6278	31.8165	0.3049	0.2581	1.4350	1.2162
21.5	2.5445	30.0374	0.1598	0.1052	0.7521	0.4955
31.0	0.3612	28.2839	+0.0221	−0.0382	+0.1040	−0.1802
40.5	− 1.8222	26.6341	−0.1028	−0.1052	−0.4838	−0.4955
50.5	− 4.1167	25.0038	−0.2213	−0.2103	−1.0415	−0.9910
59.0	− 6.0612	23.7084	−0.3114	−0.3250	−1.4656	−1.5315
68.5	− 8.2445	22.3344	−0.4029	−0.3824	−1.8962	−1.8018
78.5	−10.5945	20.9380	−0.4910	−0.3174	−2.3108	−1.4955
87.5	−12.6722	19.7918	−0.5603	−0.3059	−2.6370	−1.4414
97.0	−14.8333	18.6657	−0.6251	−0.3059	−2.9420	−1.4414

TABLE 5

$a = -6$; $p_1 = 52.3$; $q = 166.5$

% CHORD	ω(DEG.)	α(DEG.)	CAL. P	EXP. P	CAL. Q	EXP. Q
0.0	17.5388	45.9465	1.5699	....	7.3886	....
4.0	16.6000	44.3352	1.4207	1.4340	6.6864	6.7568
12.5	14.6278	42.1389	1.2177	1.1090	5.7310	5.2252
21.5	12.5445	39.6938	0.9940	0.8987	4.6782	4.2342
31.0	10.3612	37.3157	0.7799	0.7075	3.6705	3.3333
40.5	8.1778	35.1099	0.5852	0.5545	2.7542	2.6126
50.5	5.8333	32.8950	0.3950	0.4015	1.8590	1.8919
59.0	3.9399	30.2112	0.1738	0.2486	0.8180	1.1712
68.5	1.7555	29.3936	0.1086	0.1338	0.5111	0.6306
78.5	−0.5945	27.4496	−0.0418	0.0382	−0.1967	0.1802
87.5	−2.6722	26.0121	−0.1487	−0.0765	−0.6998	−0.3604
97.0	−4.8333	24.5215	−0.2551	−0.1912	−1.2006	−0.9009

TABLE 6

$a = +8$; $p_1 = 52.2$; $q = 166.5$

% CHORD	ω(DEG.)	α(DEG.)	CAL. P	EXP. P	CAL. Q	EXP. Q
0.0	3.5388	30.8738	0.2272	....	1.0693	....
4.0	2.6000	30.0841	0.1636	0.1534	0.7700	0.7207
12.5	0.6278	28.4935	+0.0381	−0.0192	0.1793	−0.0901
21.5	− 1.4555	26.9025	−0.0830	−0.1246	−0.3906	−0.5856
31.0	− 3.6388	25.3372	−0.1973	−0.2682	−0.9286	−1.2613
40.5	− 5.8222	23.8623	−0.3028	−0.3448	−1.4251	−1.6216
50.5	− 8.1167	22.4129	−0.3978	−0.4023	−1.8722	−1.8919
59.0	−10.0612	21.2492	−0.4716	−0.4598	−2.2195	−2.1622
68.5	−12.2445	20.0186	−0.5471	−0.4406	−2.5749	−2.0721
78.5	−14.5945	18.7822	−0.6186	−0.4023	−2.9114	−1.8919
87.5	−16.6722	17.7527	−0.6752	−0.4023	−3.1778	−1.8919
97.0	−18.8333	16.7457	−0.7280	−0.4023	−3.4263	−1.8919

TABLE 7

$a = -10$; $p_1 = 52.2$; $q = 166$

% CHORD	ω(DEG.)	α(DEG.)	CAL. P	EXP. P	CAL. Q	EXP. Q
0.0	21.5388	52.4299	2.1615	....	10.1729	....
4.0	20.6000	50.7048	1.9810	1.9349	9.3234	9.1218
12.5	18.6278	47.5311	1.7158	1.6284	8.0752	7.6767
21.5	16.5445	44.5904	1.4415	1.3793	6.7843	6.5026
31.0	14.3612	41.8147	1.1880	1.1494	5.5912	5.4189
40.5	12.1178	39.2137	0.9502	0.9578	4.4720	4.5157
50.5	9.8333	36.7683	0.7311	0.7950	3.4408	3.7480
59.0	7.9388	34.8769	0.5650	0.5747	2.6591	2.7094
68.5	5.7555	32.8250	0.3892	0.4693	1.8317	2.2127
78.5	3.4055	30.7617	0.2182	0.3257	1.0269	1.5353
87.5	1.3278	29.0453	0.0811	0.1916	0.3817	0.9031
97.0	−0.8333	27.6302	−0.0281	0.0479	−0.1322	0.2258

TABLE 8

$a = 14$; $p_1 = 52.2$; $q = 166$

% CHORD	ω(DEG.)	α(DEG.)	CAL. P	EXP. P	CAL. Q	EXP. Q
0.0	− 2.4612	26.1665	−0.1373	....	0.6462	....
4.0	− 3.4000	25.5038	−0.1853	−0.1149	−0.8721	−0.5419
12.5	− 5.3722	24.1589	−0.2805	−0.2586	−1.3201	−1.2192
21.5	− 7.4555	22.8192	−0.3713	−0.3448	−1.7475	−1.6257
31.0	− 9.6388	21.4984	−0.4560	−0.4406	−2.1461	−2.0772
40.5	−11.8222	20.2539	−0.5327	−0.5172	−2.5071	−2.4385
50.5	−14.1167	19.0280	−0.6049	−0.5747	−2.8469	−2.7094
59.0	−16.0612	18.0449	−0.6596	−0.6034	−3.1043	−2.8449
68.5	−18.2445	17.0079	−0.7148	−0.5172	−3.3641	−2.4385
78.5	−20.5945	15.9651	−0.7170	−0.5172	−3.3745	−2.4385
87.5	−22.6722	15.0954	−0.8086	−0.5172	−3.8056	−2.4385
97.0	−24.8333	14.2418	−0.8474	−0.4980	−3.9882	−2.3482

TABLE 9

$a = 18$; $p_1 = 52.2$; $q = 166$

% CHORD	ω(DEG.)	α(DEG.)	CAL. P	EXP. P	CAL. Q	EXP. Q
0.0	− 6.4612	23.4508	−0.3289	....	−1.5479	....
4.0	− 7.4000	22.8533	−0.3691	−0.2490	−1.7371	−1.1741
12.5	− 9.3722	21.6557	−0.4462	−0.3927	−2.1000	−1.8514
21.5	−11.4555	20.4582	−0.5202	−0.4789	−2.4483	−2.2579
31.0	−13.6388	19.2816	−0.5901	−0.5364	−2.7772	−2.5288
40.5	−15.8222	18.1657	−0.6529	−0.6135	−3.0728	−2.8901
50.5	−18.1167	17.0684	−0.7116	−0.6326	−3.3491	−2.9804
59.0	−20.0612	16.2000	−0.7554	−0.5751	−3.5552	−2.7094
68.5	−22.2445	15.2744	−0.8001	−0.5751	−3.7656	−2.7094
78.5	−24.5945	14.3355	−0.8432	−0.5560	−3.9684	−2.6191
87.5	−26.6722	13.5535	−0.8770	−0.5560	−4.1275	−2.6191
97.0	−28.8333	12.7808	−0.9087	−0.5368	−4.2767	−2.5288

TABLE 10

$a = 20$; $p_1 = 52.2$; $q = 166$

% CHORD	ω(DEG.)	α(DEG.)	CAL. P	EXP. P	CAL. Q	EXP. Q
0.0	− 8.4612	22.2013	−0.4116	....	−1.9372	....
4.0	− 9.4000	21.6393	−0.4472	−0.3834	−1.8044	−1.8063
12.5	−11.3722	20.5047	−0.5174	−0.4793	−2.4351	−2.2579
21.5	−13.4555	19.3783	−0.5844	−0.5751	−2.7504	−2.7094
31.0	−15.6388	18.2585	−0.6477	−0.6422	−3.0483	−3.0255
40.5	−17.8222	17.3068	−0.6974	−0.6901	−3.2822	−3.2513
50.5	−20.1167	16.1547	−0.7577	−0.6422	−3.5660	−3.0255
59.0	−22.0612	15.3511	−0.7965	−0.5943	−3.7486	−2.7997
68.5	−24.2445	14.4727	−0.8370	−0.5943	−3.9393	−2.7997
78.5	−26.5945	13.5819	−0.8758	−0.5943	−4.1219	−2.7997
87.5	−28.6722	12.8355	−0.9066	−0.5943	−4.2668	−2.7997
97.0	−30.8333	12.1083	−0.9354	−0.5943	−4.4024	−2.7997

TABLE 11

$a = 26$; $p_1 = 52.5$; $q = 166$

% CHORD	ω(DEG.)	α(DEG.)	CAL. P	EXP. P	CAL. Q	EXP. Q
0.0	−14.4612	18.8539	−0.6146	....	−2.8926	....
4.0	−15.4000	18.3792	−0.6410	−0.5048	−3.0168	−2.3933
12.5	−17.3722	17.4211	−0.6928	−0.5619	−3.2606	−2.6643
21.5	−19.4555	16.4692	−0.7419	−0.6190	−3.4917	−2.9352
31.0	−21.6388	15.5280	−0.7880	−0.6667	−3.6616	−3.1610
40.5	−23.8222	14.6384	−0.8295	−0.7048	−3.9040	−3.3416
50.5	−26.1167	13.7565	−0.8685	−0.6571	−4.0875	−3.1158
59.0	−28.0612	13.0461	−0.8982	−0.6381	−4.2273	−3.0255
68.5	−30.2443	12.3018	−0.9275	−0.6381	−4.3652	−3.0255
78.5	−32.5945	11.5416	−0.9559	−0.6381	−4.4988	−3.0255
87.5	−34.6722	10.8981	−0.9789	−0.6381	−4.6071	−3.0255
97.0	−36.8333	10.2716	−0.9998	−0.6381	−4.7055	−3.0255

the top of each table, as well as the value of the *dynamic pressure* q defined by $q = \frac{1}{2}\rho_1 W^2$ where ρ_1 is the density and W the magnitude of the velocity of the flow in front of the shock. In addition to the calculated values of P(Cal. P), we have given the experimental values of this quantity (Exp. P) which are obtained directly from the tables of experimental values given by Ferri.[3] We have also given in these tables the calculated and experimental values of the quantity Q (Cal. Q and Exp. Q) defined by

$$Q = 15\left(\frac{\theta - p_1}{q}\right).$$

The experimental values of Q are obtained from the tables given by Ferri by use of this relation. It is easily seen that the corresponding calculated values of Q are given by the formula

$$\text{Cal. } Q = \frac{30(\text{Cal. } P)}{\gamma M^2}.$$

The graphs of Exp. Q and Cal. Q are constructed from the data in tables 2 to 11 and appear in figures 2 to 11. Figure 2 is obtained from table 2,

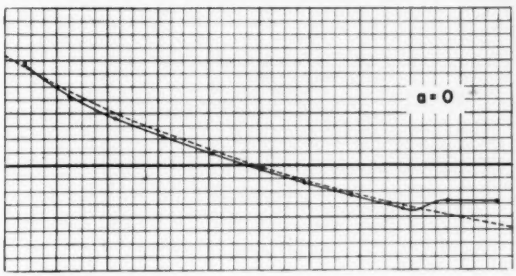

FIGURE 2

figure 3 from table 3, etc. Full lines with experimental values indicated by small circles are used for the graphs of Exp. Q; dotted lines are used for the graphs of Cal. Q. In these graphs positive values of Q, which occur at points of the profile where the pressure is greater than the pressure in front of the shock, are measured upward from the heavy line and negative values of Q, where the pressure on the profile is less than the pressure before the shock, are measured downward from this line. The length of the side of a small square in the vertical direction, along which Q is measured, represents $^1/_2$ unit; the length of the side of each large square (side lengths of four small squares) in the horizontal direction, along which per cent chord values are measured, represents 10 units. The left end of

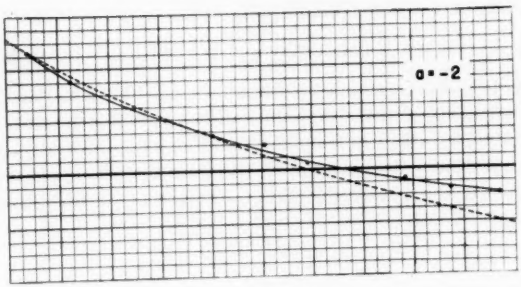

FIGURE 3

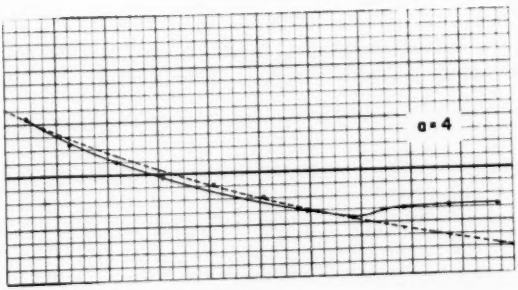

FIGURE 4

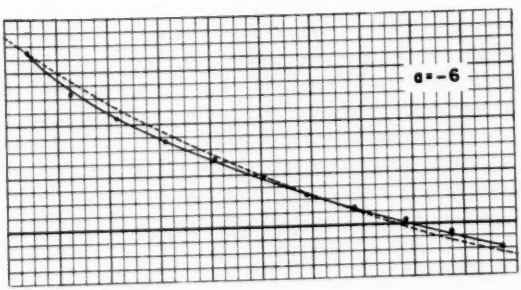

FIGURE 5

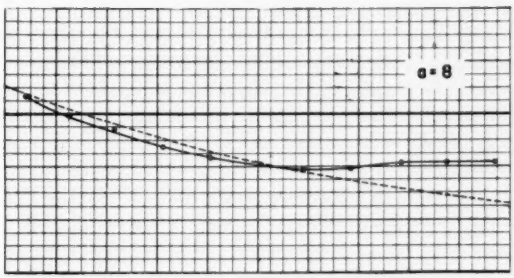

FIGURE 6

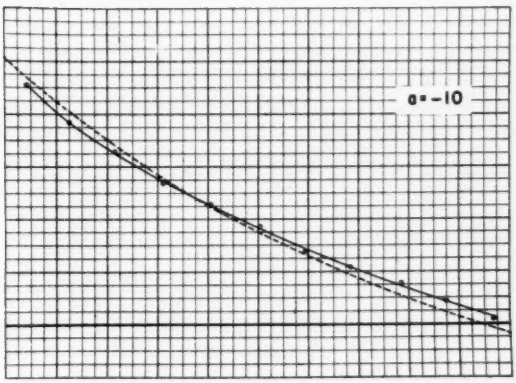

FIGURE 7

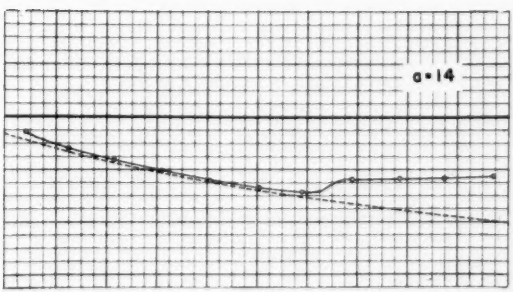

FIGURE 8

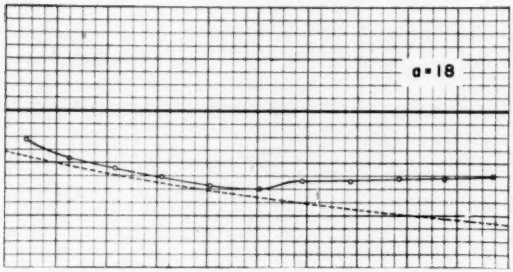

FIGURE 9

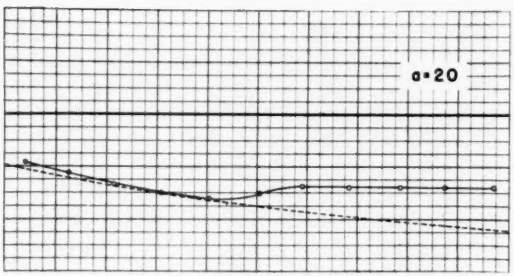

FIGURE 10

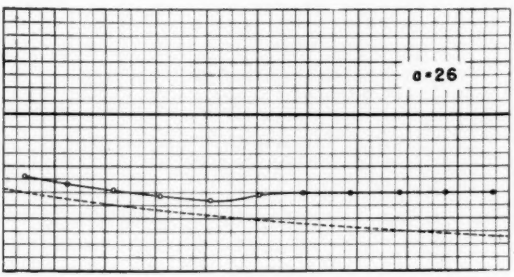

FIGURE 11

the heavy line corresponds to the 0% chord and the right end of this line to the 100% chord. The Q's rather than the P's or the direct-pressure ratios θ/p_1 are used to permit a more direct comparison between our graphs and those given by Ferri, who has employed the quantity Q for the graphical representation of his results.

3. Conclusions.—The graphs of the Cal. Q show excellent agreement with the graphs, shown in the paper by Ferri, of the calculated values of this quantity obtained by the method of flow around a corner.[4] *Hence it appears that the method of pressure calculation based on the theory of flow around a corner can be replaced, for practical purposes, by the simple formula (1).*

At certain points of the profile where the pressure is less than the pressure p_1 and the flow is expanding, a shock wave originates which causes a sudden increase in the pressure as shown on the graphs. Since this method of pressure determination makes no provision for the occurrence of such shocks, there results a considerable deviation between the calculated and experimental values of Q. Moreover, at certain points of the profile preceding these shocks differences between the calculated and experimental values of Q occur which appear too large to be attributed to experimental error. These differences can be accounted for in part by the presence of viscosity, attended by separation of flow from the boundary, which has been neglected in the theory, and in part by the obvious fact that the first approximation formula (1) cannot be expected to yield results of complete accuracy.

A determination of pressure distribution on curved profiles by the second approximation formula is now indicated. This involves the solution of an ordinary differential equation of the first order for the determination of the pressure function $\theta(\omega)$. A high-speed calculating machine is deemed advisable for the solution of this equation. If arrangements can be made for the use of such a machine the results on pressure distribution obtained will be presented in a later communication.

[1] "The Determination of Pressure on Curved Bodies Behind Shocks," to appear in *Communications on Applied Mathematics*, New York Univ. Inst. for Math. and Mech.

[2] Prepared under Navy Contract N6onr-180, Task Order No. 5, with Indiana University.

[3] Ferri, A., *Alcuni Risultati sperimentali riguardanti profili alari provati alla galleria ultrasonora di Guidonia*, Atti di Guidonia, No. 17, 1939, pp. 337–372. Translated as N.A.C.A., Technical Memorandum No. 946.

[4] See Courant, R., and Friedrichs, I. O., *Supersonic Flow and Shock Waves*, Interscience Publishers, New York, 1948, Chap. IVB, for a general discussion of the problem of flow around a corner. Specific procedures for pressure determination based on the method of flow around a corner have been given by Edmonson, Murnaghan and Snow, the Johns Hopkins University, Applied Physics Laboratory, Bumblebee Report, No. 26.

A GENIC SERIES CONTROLLING CHLOROPLAST PIGMENTS' PRODUCTION IN DIPLOID ZEA MAYS L.*

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Communicated by D. F. Jones, September 16, 1949

Introduction.—Inheritance of chlorophyll deficiencies controlled by single genes in *Zea mays* has been widely reported. Review articles by de Haan (1933)[1] and Eyster (1934)[2] describe many such cases of monofactorial control of plant pigment formation. Several studies have demonstrated the interaction of two or more genes in causing chloroplast pigment deficiencies. Lindstrom (1921)[3] described the interaction of two recessive factors termed *LLll* and *VVvv*, showing this type of inheritance:

Gentotype	Phenotype
LLvv	Virescent—white
llVV and *LLVV*	Green—normal
llvv	Yellow

Bach (1920),[4] Rasmusson (1920)[5] and Stroman (1924)[6] have also reported the existence of interacting genes which may be considered duplicate or supplementary in action. In more modern terms these would be termed suppressor gene mutants characterized by 15:1 ratios in segregating progenies. Demerec (1923, 1924, 1925, 1926)[7–10] carried out the most detailed studies of albino linkage and inheritance in maize that have been published to date. Demerec described duplicate and presumably triplicate genes for the formation of normal chloroplast pigments. Working with maize seed stocks which were segregating white and normal seedlings, Demerec demonstrated 15:1 ratio segregations in two stocks and later obtained two pedigrees which segregated in 63:1 ratios. The former condition indicates that two factors act as duplicate genes producing white seedlings in the double recessive only, while in the latter case, possibly three duplicate genes are present.

In an intriguing review of studies on the inheritance of chlorophyll, Demerec (1935)[11] suggested that qualitative differences as well as quantitative differences may occur in the various plant pigments. Such qualitative differences, it was suggested, might account for the variations in color which the maize breeder encounters as an everyday experience in observations of normal nurseries of corn inbreds (or families).

Recently, several studies concerning the inheritance of plastid pigments in *Zea mays* have attacked the problem of "physiological" or, more correctly, multigenic control of pigment formation. Elaborating upon the earlier

investigations of Emerson (1929),[12] Sprague and Shive (1929)[13] and Jenkins (1929),[14] Sprague and Curtis (1933)[15] studied the chlorophyll content as an index of the productive capacity of selfed lines of corn and their hybrids. Sprague and Curtis concluded that "mean values for chlorophyll concentration and total chlorophyll of selfed lines are reasonably reliable indices of the total yield that will be produced by their hybrids." This work, while highly suggestive, has not been entirely confirmed by the more recent studies of Miller and Johnson (1938).[16] Their research utilized larger groups of material selected from the Minnesota Corn Improvement Program. After pigment extraction and spectrophotometric determinations, evidence was obtained that a highly significant positive correlation existed between the total chlorophyll and total carotinoids in the parental inbred lines and in their F_1 crosses. However, no significant correlation could be established between the total chlorophyll concentration in the leaf tissue and the grain yield of these hybrids. Further work by Miller and Johnson (1939, 1940)[17, 18] has shown that there is no correlation between the concentration of carotinoid pigments in seed endosperm of an inbred and that in the leaf tissue of the same inbred. Moreover, maternal inheritance was shown to be insignificant when reciprocal crosses of both high and low chlorophyll inbred lines were measured for chlorophyll content. Apparently, the male and female parents contributed equally to the F_1 crosses in respect to chlorophyll concentration. Hence, genotype in these studies determines phenotype without significant cytoplasmic or plastid influence.

Experimental Materials.—The problem of chlorophyll inher tance involves an understanding of the chloroplast pigments, their genic control and their correlation to plant production. Six *Zea mays* inbreds of varying phenotypic chlorophyll appearance were chosen: Dark (inbreds designated *C*106 and *T*1), Medium (*A*158 and *C.I.* 4–8) and Light (*W*23 and *Os*420). Chloroplast pigments were extracted and measured from seedlings of both the selected inbreds and F_1 generation seedlings of these inbreds crossed with a tester stock. This tester stock contributed both a pleiotropic gene and a suppressor gene mutation to the F_1 chlorophyll test crosses. Since an understanding of these genic types as well as the duplicate gene type is necessary for a clear comprehension of the results and discussion to be presented, the following definitions are given (after Knight, 1948)[19]:

Pleiotropism: The controlling of more than one character by a single gene. (This may also be termed Genuine Pleiotropism.)

Suppressor Mutation: A sudden change occurring at a particular chromosomal locus such that a gene is formed capable of nullifying the effect of a particular major gene.

Duplicate Gene: Identical genes but situated at different loci and showing no cumulative effect.

Polymeric Genes: Non-allelic genes governing the same character and having a similar effect on it.

Extraction of the plant pigments followed the analytical methods and utilized the constants for calculating total amounts of pigment presented by Griffith and Jeffrey (1944).[20] However, use of Skellysolve-B, a purified petroleum ether, as the solvent for all plant pigments extracted was found to expedite the entire procedure and thus reduce the time involved, and permit a larger number of samples to be run.

Since the absorption maxima obtained from Beckman spectrophotometric determinations of pigment extracts tended to be the same or very similar to those utilized by Griffith and Jeffrey, and since reproducibility of results was good, it was felt that quantitative calculations based on their formulae probably give a fair approximation of the pigment amounts present in the original seedlings.

Data from field plantings to be presented in conjunction with the plant pigment extractions and the segregation ratio counts (from seedlings grown under conditions of constant light and temperature) were based on Latin squares prepared by Fisher and Yates (1938).[21]

Experimental Results.—Table 1 presents the data from extracts of the six field corn inbreds while table 2 shows data from extracts of these six inbreds crossed by the tester stock. This tester was chosen because the line carries a pleiotropic gene that causes a kernel endopserm color change, wherein the germinated light kernel type yields a chlorophyll deficient seedling, while the dark kernels germinate to give perfectly normal plants.

TABLE 1*

INBRED	USUAL PHENOTYPE	CHLOR. *a*, MG./G.	CHLOR. *b*, MG./G.	TOTAL CHLOR., MG./G.	% *a* CHLOR.	TOTAL CAROTENE, MG./G.	XAN., K./G.
*Os*420	Light	0.764	0.556	1.320	57.9	0.068	0.032
*W*23	Light	0.613	0.138	0.751	81.6	0.040	0.025
*A*158	Medium	0.699	0.102	0.801	87.3	0.057	0.026
C.I. 4–8	Medium	0.688	0.262	0.950	72.4	0.047	0.023
*T*1	Dark	0.768	0.303	1.071	71.7	0.070	0.027
*C*106	Dark	0.762	0.456	1.218	62.6	0.055	0.030

* Average of duplicate samples—based on fresh weight.

A second gene which tends to overcome the chlorophyll suppression action of the pleiotropic gene is also present in the tester stock. These genes act independently of each other. Hence, the suppressor gene mutant segregates within the progeny of the light kernels and because it is incompletely dominant, three chlorophyll color classes are detectable in these plants. The classes are designated as albino (white), light-green (yellow-green) and pseudo-normal (practically a normal green). The suppressor gene does not affect the endosperm color variation brought about through the action of the pleiotropic gene nor does it overcome the lethal

effect of the pleiotropic gene for after a few weeks the pseudo-normal seedlings take on a watery appearance and quickly die off.

The F_2 segregating progenies of the original inbred color lines crossed by the tester stock and subsequently selfed, showed that the light and medium inbreds (*W*23, *Os*420, *A*158, *C.I.* 4–8) contained normal alleles of the pleiotropic gene and recessive alleles of the suppressor gene mutant in the homozygous state. However, the dark inbreds (*T*1 and *C*106) were shown to have both the pleiotropic gene and the suppressor gene

TABLE 2*

TEST CROSS	PHENOTYPES CROSSED	CHLOR. *a*, MG./G.	CHLOR. *b*, MG./G.	TOTAL CHLOR., MG./G.	% *a* CHLOR.	TOTAL CAROTENE, MG./G.	XAN., K./G.
*Os*420 × tester	Light × Medium	0.641	0.306	0.947	67.7	0.052	0.020
*W*23 × tester	Light × Medium	0.531	0.118	0.649	81.8	0.038	0.018
*A*158 × tester	Medium × Medium	0.650	0.228	0.878	74.0	0.046	0.024
C.I. 4–8 × tester	Medium × Medium	0.671	0.217	0.888	75.6	0.041	0.023
*T*1 × tester	Dark × Medium	0.650	0.258	0.908	71.6	0.050	0.018
*C*106 × tester	Dark × Medium	0.573	0.494	1.067	53.7	0.049	0.020

* Average of duplicate samples—based on fresh weight.

TABLE 3

SEEDLING SEGREGATION—F_2 GENERATION OF SELFS OF INBRED *W*23 CROSSED BY THE TESTER STOCK (ONLY LIGHT KERNELS PLANTED)

EAR NO.	NO. SEED PLANTED	No. SEED GERMINATED	ALBINO OBS.	ALBINO EXP.	LIGHT-GREEN OBS.	LIGHT-GREEN EXP.	PSEUDO-NORMAL OBS.	PSEUDO-NORMAL EXP.	X^2
1	50	50	10	12.50	28	25.00	12	12.50	0.88
2	50	50	12	12.50	24	25.00	14	12.50	0.24
3	50	48	10	12.00	23	24.00	15	12.00	1.12
4	50	47	9	11.75	23	23.50	15	11.75	1.55
5	50	47	18	11.75	19	23.50	10	11.75	4.44
Totals	250	242	59	(60.50)	117	(121.00)	66	(60.50)	

X^2 based on individual ears (expected ratio 1:2:1) = 8.23, where $D.F.$ = 10 shows $P.$ = 50–95%.

X^2 based on totals of all ears = 0.67, where $D.F.$ = 2 shows $P.$ = 50–95%.

mutant in the homozygous state. In addition to the two chloroplast pigment controlling genes, it was seen that the dark lines contained a third completely dominant gene for normal chlorophyll production which incidentally tended to overcome the lethal effect of the pleiotropic gene.

This gene may be considered to be semi-duplicate to the pleiotropic gene in that it completely masks the latter's effect upon plant pigment production while the endosperm color effect is unchanged. Tables 3 and 4 show two representative counts of seedling types—one from a light type (*W*23) and one from a dark type inbred (*T*1).

TABLE 4

SEEDLING SEGREGATION—F_2 GENERATION OF SELFS OF INBRED *T*1 CROSSED BY THE TESTER STOCK (ONLY LIGHT KERNELS PLANTED)

EAR NO.	NO. SEED PLANTED	NO. SEED GERMINATED	ALBINO-LIGHT GREEN OBS.	ALBINO-LIGHT GREEN EXP.	PSEUDO-NORMAL OBS.	PSEUDO-NORMAL EXP.	NORMAL OBS.	NORMAL EXP.	X^2
1	50	50	0	...	10	12.50	40	37.50	0.67
2	50	48	0	...	9	12.00	39	36.00	1.25
3	50	49	0	...	10	12.25	39	36.75	0.55
4	50	50	0	...	11	12.50	39	37.50	0.24
5	50	50	0	...	11	12.50	39	37.50	0.24
6	50	50	0	...	13	12.50	37	37.50	0.03
Totals	300	297	0	...	64	(74.25)	233	(222.75)	

X^2 based on individual ears (expected ratio 3:1) = 2.98, where $D.F.$ = 6 shows $P.$ = 50–95%.

X^2 based on totals of all ears = 1.88, where $D.F.$ = 1 shows $P.$ = 10–20%.

In the summer of 1948 the six F_1 test crosses (chlorophyll inbreds *X* tester stock) were entered in a 6 × 6 Latin square field trial. Rows were planted thickly and later thinned to a uniform stand so that variation in the total number of plants per entry was not a factor in the yields obtained. Single cross yields as well as other pertinent data from this trial are presented in table 5.

TABLE 5

YIELD TRIAL—PLANTED MAY 20, 1948; HARVESTED OCT. 29, 1948

ENTRY	TOTAL PLANTS	*YIELD, POUNDS AT 15.5% MOISTURE CONTENT	MATURITY, DAYS
*T*1 × tester	174	75.7	77
*C*106 × tester	166	67.5	77
*Os*420 × tester	169	63.5	76
*A*158 × tester	171	62.1	73
*W*23 × tester	167	61.8	75
C.I. 4–8 × tester	171	55.2	79

* *Just significant difference* = 11.1 pounds at 0.05*P*.

Several significant correlations may be noted in the pigment extraction data and grain yield figures and these significant correlations may be seen to be dependent upon the pigment controlling genomes of the inbreds involved. These correlations may be summed up as follows:

	VALUES COMPARED	DEGREES OF FREEDOM	"R" VALUES	SIGNIFICANCE
1.	Total carotene (inbreds):total carotene (single crosses)	4	+0.934	High positive correlation
2.	Total chlorophyll (inbreds and single crosses):total carotene (inbreds and single crosses)	10	+0.733	High positive correlation
3.	Ratio of chlorophyll *a*/total carotene (inbreds and single crosses):yield in pounds of grain (single crosses only)	10	−0.639	Significant negative correlation

These correlations are in agreement with previous work but show in addition that the ratios between the chloroplast pigments are of significant importance in determining plant productivity (on a grain basis in this case).

Discussion.—The way in which a chloroplast is synthesized would seem to have a direct influence on the way in which it functions in the process of photosynthesis. This being true, the study of plants in which mutations have occurred in chloroplast synthesis is also a study of plants in which the photosynthetic capacities have been altered to a greater or lesser degree. The data presented demonstrate that even in inbred lines of diploid *Zea mays* the genes controlling the production of the chloroplast pigments are quite variable. Undoubtedly the discovery and isolation into separate progeny as shown in the segregating seedling types (tables 3 and 4) presage the finding of a series of genes controlling the formation of the chloroplast skeleton and, subsequently, the chloroplast pigments. It is suggested that such a series be designated Cl_1cl_1, Cl_2cl_2, Cl_3cl_3, . . . Cl_zcl_z. Thus, the three genes described may be symbolically represented as follows:

TYPE OF GENE	SUGGESTED DESIGNATION
Pleiotropic	Cl_1cl_1
Suppressor gene mutant	Cl_2cl_2
Semi-duplicate	Cl_3cl_3

Utilizing the new series of designations, it is seen that originally the light and medium inbreds, *Os*420, *W*23, *A*158 and *C.I.* 4–8, had the genotype Cl_1Cl_1, cl_2cl_2, cl_3cl_3 while the dark inbreds, *T*1 and *C*106, had the genotype Cl_1Cl_1, Cl_2Cl_2, Cl_3Cl_3 and the tester stock genotype was Cl_1cl_1, Cl_2Cl_2, cl_3cl_3. These genotypes show that the dark lines vary from the light and medium inbreds in two of the three genes tested. This variation undoubtedly accounts for the fact that while plants of the light and medium lines are often transitional in color, the dark inbreds are always distinguished from the medium and light lines with ease. It is probable that unidentified modifying genes cause the color variation between the light and medium lines.

From this evidence, it seems probable that the variation in genes controlling the relative amounts of the chloroplast pigments accounts for the

distinct variation in inbred color and, through alteration of photosynthetic capacities, for the significant differences in grain production in the single crosses with the tester stock. Work is now in progress to determine chromosome loci of the three genes described and to discover and isolate other genes of the pigment control series. These data as well as a more complete publication concerning the genetic, economic and evolutionary importance of this genic series will be prepared in the near future.

* An abstract of a dissertation presented for the degree of Doctor of Philosophy in Yale University.

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*REPRODUCTION AND DISTRIBUTION OF THE CYTOPLASMIC FACTOR FOR MALE STERILITY IN MAIZE**

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Recent work of Preer,[1, 2] Sonneborn[3, 4] and L'Héritier,[5, 6] has emphasized and helped clarify the rôle of the cytoplasm in the determination and inheritance of characters. The present paper deals with the inheritance of a cytoplasmic factor in maize in such a way as to determine particle number, rate of reproduction of the particle and the distribution of the particles

within the plant. This is the same cytoplasmic factor previously studied by Rhoades.[7] Similar cytoplasmic factors causing male sterility have been found in onions by Jones and Clarke[8] and in sugar beets by Owen.[9] In both of these latter cases, an interaction between the cytoplasmic factor and chromogenes was reported.

Rhoades[7] showed that microsporogenesis was normal and that the abortion occurred during the development of the microspore into a mature male gametophyte. If the plant was partially fertile, certain of these microspores would continue development normally. When this partially fertile pollen was used in cross-pollinations there was no evidence of a transfer of the male sterile factor. This fact suggested the possibility of the presence of one or more cytoplasmic factors in a microspore destined to abort and the complete absence of the factor in those microspores which would develop into normal pollen grains.

Partially fertile lines were selected for a detailed study of variability in pollen production among florets of a given plant. Such a study would rule out the possibilities of genic and physiological differences which might normally arise in a comparison between plants. The use of partially fertile plants makes possible the detection of small differences not measurable in completely sterile lines.

The amount of viable pollen was determined by smearing the pollen from the anthers of a single floret in a drop of aqueous iodine-potassium iodide solution. Those pollen grains which were plump and full of starch were considered viable. If there were any shrunken, starch-deficient or otherwise aborted areas in the pollen grain, it was considered to be non-viable. Cross-pollinations using the partially fertile types as pollen parents were successful in direct proportion to the amount of viable pollen shed per plant as determined by this method.

Five tassels from partially fertile plants were chosen at random. The per cent of viable pollen was determined by observing 150–200 pollen grains per floret, using a Breed micrometer to limit the amount of the field counted. Counts were made at a magnification of 150 ×. Five such counts at random usually included 150–200 pollen grains. When such data from any individual tassel were subjected to a $2 \times N$ chi square test, the variation among the florets exceeded that expected by chance ($P = <0.001$). Frequency distributions were made of the percentages of good pollen produced in these florets. Such frequency distributions were bimodal or polymodal with only one approaching unimodality. The modes of these distributions were at 36 and 60 per cent viable pollen. Figure 1 presents these data combined to show these peaks more clearly.

Each of the five plants used in figure 1 when studied by itself was free of genic and physiological differences so that such polymodal differences must have been due to the cytoplasmic factor itself. Since the modes

from these five plants were at the same points it would indicate that the same system was involved in each case.

An explanation for such a distribution may be formulated in the following manner. Assume the presence of k discrete cytoplasmic particles in the microsporocytes which give rise to aborted pollen grains. Since functional pollen produced by a partially fertile plant does not transfer the cytoplasmic factor it can be assumed to be free of the male sterile particle. It follows that the aborted pollen grains contain one or more of these particles. The particle number must remain constant through successive cell divisions. If, at mitosis, the particles were distributed to daughter cells by chance alone, cells should arise devoid of the particle. The descendents of such a cell should all be devoid of particles and a

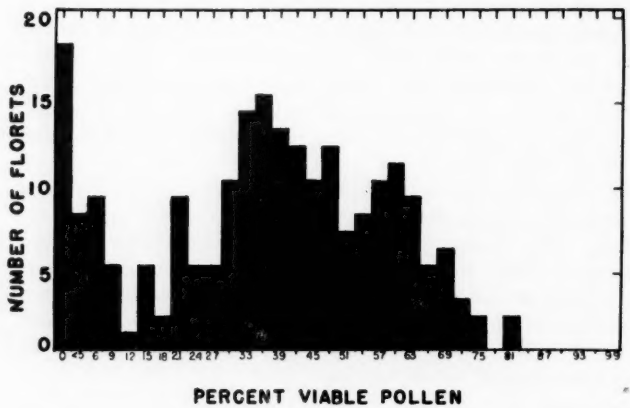

FIGURE 1

Frequency distribution of number of florets plotted against percentage of viable pollen, grouped in intervals of 3 per cent, accumulated from 5 plants.

pollen fertile chimera should result. No such chimeras have been found in any of the plants tested. From inspection of the variability in figure 1, it is evident that at some late cell division, such as during meiosis, the control which previously had insured equal division must be impaired. If this distribution at meiosis were random, a Poisson series would be expected.

The Poisson series is the basic discontinuous random distribution. It may occur when a variable is not able to take all possible values, but is confined to a particular series of values, such as whole numbers. If a variate can take the values 0, 1, 2, . . . , X, . . . , and the relative frequencies with which the values occur are given by the series

$$e^{-m}\left(1, m, \frac{m^2}{2!}, \ldots, \frac{m^x}{x!}, \ldots\right)$$

then the number is distributed in the Poisson series.[10] The mean is the only unknown parameter of the Poisson series. If m is the mean number of particles per pollen grain, the proportion of samples containing none is e^{-m}. The pollen grains, free of the particle, would be viable. If each peak (Fig. 1) represented the mean of a component Poisson series, the average number of particles per pollen grain would be $^1/_2$ and 1 for 60 and 36 per cent viable pollen, respectively.

If the number of particles per cell were constant throughout the plant and only two types of pollen could be identified, pollen free of the particles and pollen containing one or more particles, it should be possible to plot the percentage of viable pollen in successive samples as a unimodal frequency distribution. Figure 1 is polymodal although only two modes predominate.

Two possibilities may explain such a divergence from the Poisson. Occasionally particle division and cell division might not coincide during mitoses, leading to an increase or decrease in the number of particles per daughter cell. Alternately, the distribution of particles to daughter cells may not always be exact.

Either of these possibilities could lead to a heterogeneous population of particles within the cells of a single plant. Random samples drawn from such a population would take the form of a negative binomial distribution.[11] In experimental sampling the negative binomial arises from a single extension of the conditions underlying the Poisson series. The Poisson series arises when equal samples are taken from perfectly homogeneous material. It is completely determined by the average number of particles, m per sample. If unequal samples were taken, or, if the material was not perfectly homogeneous, the value of m would vary from sample to sample.

If an atypical division happens only occasionally, a stage should be reached as meiosis is approached where a significant discrepancy in particle number and consequently in the percentage of viable pollen would be expected in some cases and not in others. This can be tested by comparing the percentages of good pollen in the anthers of the two florets which comprise the spikelet. Although still many cell divisions from meiosis, the anthers represent a much later common derivation than can be claimed for florets on different spikelets. In consequence, a $2 \times N$ chi square test should show agreement with the binomial in some cases and not in others. Comparison of the viable pollen in the anthers of the five spikelets studied showed probabilities of 0.78, 0.22, <0.01, <0.001 and <0.001. This shows that a binomial distribution is fit occasionally as meiosis is approached which is in agreement with the proposed hypothesis.

If the male sterile factor is distributed at random during microsporogenesis, it is of fundamental interest to see what type of distribution is had during megasporogenesis. Is this random distribution a function of meiosis?

This problem was tested by studying six florets (at random) from each of 78 plants from a three-way cross. These data are shown graphically in figure 2.

In making such counts the accuracy is very limited below 10 per cent and above 90 per cent. Actual counts were only made on those florets about 5 per cent or more viable. It should be noted that three definite peaks can be found at 15, 36 and 57 per cent. This is in agreement with

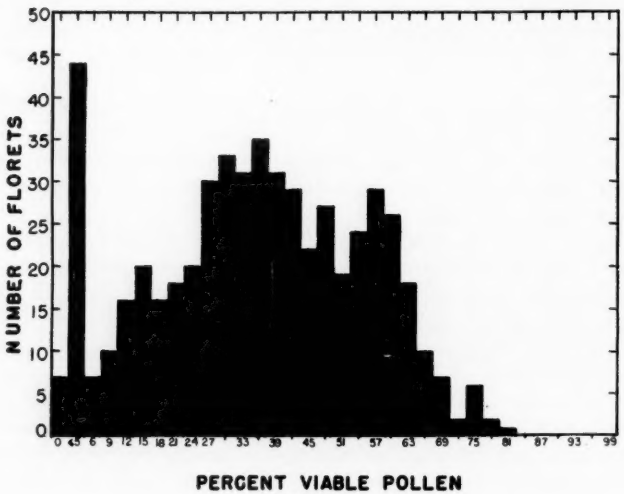

FIGURE 2

Frequency distribution of number of florets plotted against percentage of viable pollen, grouped in intervals of 3 per cent, accumulated after determining per cent of good pollen in 6 florets at random on each of 78 plants.

mean particle numbers of 2, 1 and $^1/_2$, respectively. It should also be noted that the variability is greater in figure 2 than in figure 1, which indicates that the random distribution probably took place at megasporogenesis of the parent plant as well as microsporogenesis of the progeny and is a function of meiosis.

The female plant in the three-way cross used in this study produced 49 per cent viable pollen in 1947. This corresponds to 0.714 particle per pollen grain. The median of the florets (Fig. 2) was 0.741 particle. In

a second study the female had 0.891 particle per pollen grain (1947) and the progeny 0.967 particle per pollen grain (1948). These data suggest that there was no appreciable increase or decrease in the number of particles per cell during the life cycle of these two families.

One of the basic premises of the Poisson series is that the variate must be confined to a particular series of values, such as whole numbers. If the number of particles per cell must be one or more (as shown previously by the absence of pollen fertile chimeras), a mean number of $^1/_2$ needs to be justified.

The assumption that the particle number is relatively constant at mitosis seems to be valid. It has also been assumed that at some stage, presumably at meiosis, the forces in control during mitosis are absent and distribution of the particle becomes random. Since the division of particles presumably paralleled that of the chromosomes during mitosis a similar parallelism during meiosis would suppress particle division at the same time and lead to the random distribution of undivided particles. If the cytoplasmic particles were to divide only once during meiosis as do the chromosomes, a mean number of 1 per somatic cell will be reduced to $^1/_2$ per microspore. Similarly, peaks arose at $^1/_2$ and 1 particle per microspore. Never was there any variance from this distribution. Therefore, the numerical difference between these peaks ($^1/_2$) should be the equivalent of a whole particle per somatic cell. Similarly modes were not found between 0 and $^1/_2$ particle per cell.

Discussion.—The significance of plasmagenes has been the subject of much speculation. Sonneborn[12] has recently reviewed the numerous views presented by many workers. From the evidence presented here it is possible to characterize partially the cytoplasmic factor causing male sterility in corn.

The male sterile factor is particulate. If it were not a whole unit or particle its distribution would not follow a negative binomial made up by a series of Poisson distributions.

The reproduction and distribution of this particle are quite similar to the reproduction and distribution of chromosomes. The similarity in reproduction holds both at meiosis and mitosis. The similarity of distribution holds quite well at mitosis but is completely random at meiosis. It must, therefore, have many characteristics in common with the chromosome. It might also be suggested that this is a virus. All attempts to transfer it artificially have failed. It is doubtful that a virus would be so dependent on chromosome division for its reproduction and distribution.

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*THE EFFECT OF OXYGEN ON THE FREQUENCY OF X-RAY INDUCED CHROMOSOMAL REARRANGEMENTS IN TRADESCANTIA MICROSPORES**

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The recent studies of Thoday and Read,[1] using root tips of *Vicia faba*, indicate that the availability of oxygen to cells is a very important factor in radiosensitivity. Under anaerobic conditions, sensitivity to x-rays is markedly reduced, as measured both by inhibition of growth and by frequency of anaphase figures showing chromosome aberrations. The results of Hayden and Smith[2] on x-radiation of barley seeds in a vacuum also suggest that the absence of oxygen results in reduced radiosensitivity. In view of these results it seemed of interest to test the effect of oxygen on the frequency of x-ray induced chromosomal rearrangements in Tradescantia, especially since there is already available a wealth of information on radiation effects in this organism as a result of the pioneer investigations of Sax[3] which, together with those of other investigators, have been summarized by Lea[4] and by Catcheside.[5]

Materials and Methods.—*Tradescantia paludosa* Anderson and Woodson, clone 5 of Sax, was used in all experiments. Observations were made at the first postmeiotic mitosis in the microspore by means of acetocarmine smear preparations at the four- to five-day interval following treatment, at which time only chromosome-break types are present. The principal aberration types analyzed at this period are interchanges (dicentrics and centric rings). In addition, interstitial deletions (intercalary deletions or isodiametric fragments) are numerous. Acentric rings and terminal deletions were also recorded but, because of their comparative rarity, were not used in later calculations.

The x-ray source, a Coolidge self-rectifying tube with tungsten target was operated at 250 kvp. and 15 ma. The inherent filtration was equivalent to 3 mm. aluminum. In addition, all exposures were made inside a lucite exposure chamber whose top was $^1/_4$-inch thick. The inflorescences were inserted in an upright position through holes in a very thin lucite platform in the center of the box in order to insure uniform exposures and to avoid back-scattering. Dosages were measured inside the exposure chamber at the position of the inflorescences with a 100-r Victoreen thimble ionization chamber recently calibrated by the U. S. Bureau of Standards. In all experiments, unless otherwise noted, the dosage rate was constant, 45 r/min.–different total dosages being administered by increasing the time of exposure.

In order to make exposures in different gases, inflorescences were first placed in a suction flask, evacuated with a water pump for approximately two and one-half minutes, and the appropriate gas then admitted into the flask. This procedure was repeated five times. The purpose of this operation was to remove the air enclosed by the sepals and petals of the buds. The inflorescences were then quickly placed in the lucite exposure chamber, which could be made airtight, the air evacuated and the appropriate gas admitted. This operation was performed twice. The lucite chamber was next placed in the x-ray machine and the inflorescences irradiated at room temperature. After exposure, the inflorescences were kept in the gas chamber for approximately ten minutes, following which they were removed, reëvacuated in the suction flask and air permitted to diffuse in. This procedure was repeated five times, as previously. Commercial cylinders of the various gases were utilized, the indicated purity in all cases being at least 99.5%.

In the first control experiment in which inflorescences were exposed to x-rays in air inside the lucite chamber, the same initial series of evacuations was carried out, except that air rather than some other gas was permitted to enter the flask following each evacuation. A repetition of this control experiment in air without prior evacuation of the buds gave essentially similar results indicating that the evacuation procedure itself did not modify the results. Observations of other control buds, exposed to atmospheres of nitrogen, oxygen and other gases in an identical manner but not x-rayed, indicated that exposure to the gas alone did not result in any detectable cytological abnormalities.

In general from 10 to 15 inflorescences were exposed at each treatment and as many slides as possible made at the four- and five-day interval following irradiation. The aberration frequency for each dosage was calculated from the total number of interchanges and interstitial deletions recorded in either 50 or 100 cells on 3 to 15 (average ca. 7) slides. Chi-square tests did not reveal any excess variation among slides from one treatment

and standard errors were calculated by the method discussed by Catcheside, Lea and Thoday.[6]

Results and Discussion.—The results of comparative experiments in which inflorescences were irradiated in air, in nitrogen and in oxygen are presented in table 1 and shown graphically in figures 1 and 2. All the data in experiment 1 (exposures in air) were obtained by one investigator (N. H. G.). Combined data from the scorings of both investigators for interchanges (dicentrics and centric rings) are given in all succeeding experiments since the scorings of these aberration types by both investigators are quite comparable. However, there is considerable individual variation

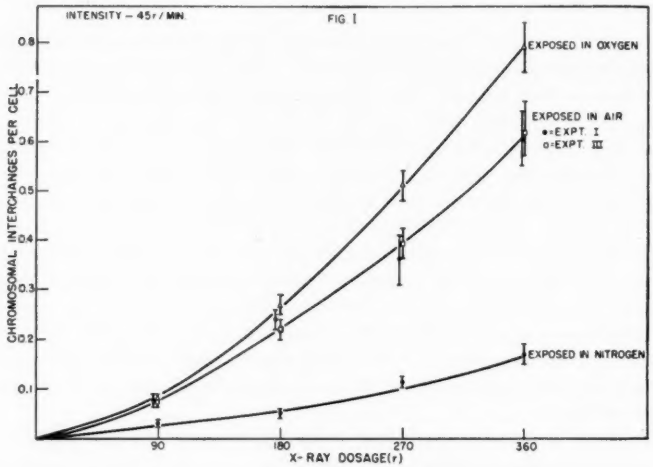

FIGURE 1

X-ray dosage curves for interchanges (dicentrics and centric rings) induced in Tradescantia microspores exposed in atmospheres of air, nitrogen and oxygen. Vertical bars indicate limits of standard errors.

in the scoring of interstitial deletions because of the small size of some of these aberration types and the more extensive data of only one investigator (H. P. R.) have been used in all except the first experiment. In general, these values are lower than those obtained in comparable scorings by the other author (N. H. G.) by approximately 20%. Despite this, the relative differences from one experiment to another are consistent in both sets of data.

It is clear from these data that the aberration frequency is strikingly reduced when exposures are made in nitrogen instead of in air. Further,

there is a significant though not as marked a difference when oxygen is used in place of air, the result in this instance being an increased aberration yield. The magnitude of these differences is very considerable, the increase in both interchanges and deletions in exposures made in oxygen as compared with nitrogen being as much as fivefold at higher dosages. These results strongly suggest that the presence of oxygen has a marked influence in increasing radiosensitivity in this material as measured by chromosomal aberration frequency.

There is no reason to believe that the observed effects can be accounted for by a modification of the timing of the cell cycle as a result of exposure

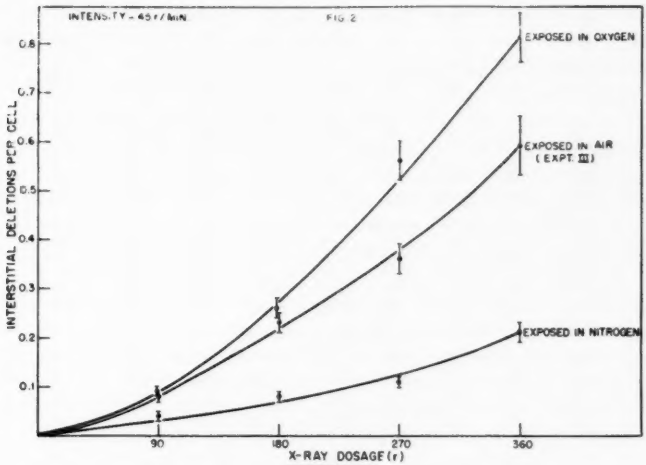

FIGURE 2

X-ray dosage curves for interstitial deletions induced in Tradescantia microspores exposed in atmospheres of air, nitrogen and oxygen. Vertical bars indicate limits of standard errors.

to the different gases such that variations in mitotic sensitivity are involved. Observations of the x-ray effects were not made until the fourth and fifth days following treatment, by which time any effect of a possible acceleration or retardation of the mitotic cycle should have little if any consequence. It has been shown by Sax[3] that there is very little change in x-ray sensitivity throughout the five- to six-day-long resting stage. Further, there is no evidence from the present data of significant differences in aberration frequencies in comparisons of four- and five-day material within individual experiments.

In order to eliminate the possibility that the presence of nitrogen rather than the absence of oxygen might be responsible for the observed decrease in radiosensitivity, further experiments were performed in which other gases

TABLE 1

FREQUENCIES OF INTERCHANGES AND INTERSTITIAL DELETIONS INDUCED IN TRADESCANTIA MICROSPORES EXPOSED TO X-RAYS IN AIR, IN NITROGEN AND IN OXYGEN ALL DOSAGES ADMINISTERED AT A CONSTANT INTENSITY OF 45 R/MIN.
(For further discussion, see text)

DOSE	CELLS SCORED	DICENTRICS	CENTRIC RINGS	TOTAL UNTERCHANGES	INTERCHANGES PER CELL	CELLS SCORED	INTERSTITIAL DELETIONS	INTERSTITIAL DELETIONS PER CELL
				EXPOSED IN AIR (EXPT. 1)				
90	500	29	11	40	0.08 ± 0.01	500	48	0.10 ± 0.01
180	276	45	20	65	0.24 ± 0.03	276	71	0.26 ± 0.03
270	150	44	10	54	0.36 ± 0.05	150	76	0.51 ± 0.06
360	200	92	29	121	0.61 ± 0.06	200	144	0.72 ± 0.06
				EXPOSED IN NITROGEN				
90	1150	23	9	32	0.03 ± 0.005	800	32	0.04 ± 0.01
180	400	15	4	19	0.05 ± 0.01	400	30	0.08 ± 0.01
270	1267	107	40	147	0.12 ± 0.01	800	90	0.11 ± 0.01
360	450	59	20	77	0.17 ± 0.02	450	93	0.21 ± 0.02
				EXPOSED IN AIR (EXPT. 3)				
90	1050	52	30	82	0.08 ± 0.01	800	65	0.08 ± 0.01
180	600	88	44	132	0.22 ± 0.02	600	139	0.23 ± 0.02
270	600	165	73	238	0.40 ± 0.03	400	143	0.36 ± 0.03
360	150	68	25	93	0.62 ± 0.06	150	88	0.59 ± 0.06
				EXPOSED IN OXYGEN				
90	800	50	15	65	0.08 ± 0.01	800	72	0.09 ± 0.01
180	900	165	77	242	0.27 ± 0.02	900	231	0.26 ± 0.02
270	500	175	78	253	0.51 ± 0.03	350	195	0.56 ± 0.04
360	300	157	80	237	0.79 ± 0.05	300	244	0.81 ± 0.05

TABLE 2

FREQUENCIES OF CHROMOSOMAL INTERCHANGES AND INTERSTITIAL DELETIONS INDUCED IN TRADESCANTIA MICROSPORES EXPOSED TO 360 R AT 45 R/MIN. IN ATMOSPHERES OF NITROGEN, ARGON AND HELIUM

TREATMENT	CELLS SCORED	DICENTRICS	CENTRIC RINGS	TOTAL INTERCHANGES	INTERCHANGES PER CELL	CELLS SCORED	INTERSTITIAL DELETIONS	INTERSTITIAL DELETIONS PER CELL
360 r in nitrogen	500	96	36	132	0.26 ± 0.02	150	56	0.19 ± 0.05
360 r in argon	500	130	50	180	0.36 ± 0.03	300	164	0.27 ± 0.04
360 r in helium	300	38	14	52	0.17 ± 0.02	150	40	0.13 ± 0.04

were substituted for nitrogen. The results of such an experiment are presented in table 2. In this instance, comparative exposures were made at a single dose, 360 r at 45 r/min., in nitrogen, in helium and in argon. It will

be noted that helium is even more effective than nitrogen in this experiment in reducing the frequency of interchanges and deletions, the values obtained in this gas being as low as or lower than those found in the nitrogen exposure at 360 r in the first series of experiments. The value for interchanges in nitrogen is somewhat higher in this experiment than in the previous one, but is still markedly less than that obtained in air. The aberration frequencies in argon, although much lower than those in air, are higher than those obtained in nitrogen or helium. The reason for this difference is not apparent but is probably due to uncontrolled variables in the experimental techniques. It is clear from this experiment, however, that the reduced aberration frequencies as compared with air cannot be attributed to the presence of a particular gas, such as nitrogen, but must result from the absence of oxygen.

As yet no exposures in atmospheres of oxygen of known intermediate percentage composition, such as 5 or 10%, have been attempted. However, some experiments were performed in which the oxygen percentage was probably close to these intermediate values. These results were inadvertently obtained when an undiscovered air leak was present in the lucite exposure box resulting in a mixture of air and the gas being introduced. The interchange frequencies per cell at 360 r (45 r/min.) under these conditions were all intermediate between those obtained in exposures made in air and in the pure gases. These values were as follows: nitrogen, 0.43 ± 0.03; helium, 0.54 ± 0.03; argon, 0.52 ± 0.03 and 0.44 ± 0.03 (different experiments). The frequencies of interstitial deletions were also intermediate between those obtained in air and in the pure gases. The values (H. P. R. only) were: nitrogen, 0.53 ± 0.04; helium, 0.41 ± 0.03; argon, 0.42 ± 0.04 and 0.32 ± 0.03. It thus appears clear that the aberration frequency increases as the percentage of oxygen increases, but it is not yet possible to make a quantitative evaluation of this relation.

In attempting to interpret the mechanism by which oxygen increases the radiosensitivity of Tradescantia chromosomes, it is immediately necessary to decide whether this effect results from an increase in the initial frequency of x-ray-induced breaks or from an effect on the reunion of broken ends, such that recombination is favored over restitution. It is of course possible that both of these effects may be present. A preliminary analysis of the dosage curves for interchanges at a constant intensity of 45 r/min. utilizing Lea's[4] formulation for the recovery time, τ,[7] suggests that the oxygen effect may be exerted principally by way of the recovery mechanism. However, it appears necessary to perform further exposures at higher and lower intensities in order to obtain more data on this point. Additional evidence is also being sought by means of another experimental approach. Previous investigations of a number of workers have indicated that in Tradescantia x-ray-induced chromosome breaks may remain open (i.e., available for participation in interchanges) for a considerable period of time. The

average restitution time as calculated by Lea[4] is about four minutes. Thus it should be possible, if oxygen exerts its effect on the recovery mechanism so as to favor recombination, to increase the yield of rearrangements by transferring inflorescences irradiated at high intensity in nitrogen to oxygen as soon as possible after exposure. An initial attempt to perform such an experiment has not been conclusive. Buds were evacuated and nitrogen admitted in the usual fashion. The buds were then exposed to 300 r at 200 r/min. in the lucite box in air in order to facilitate removing half of the inflorescences to oxygen as rapidly as possible at the end of the irradiation. This transfer required approximately one minute. It was found that the frequency of interchanges was the same in both the control half (remaining in the lucite chamber) and in the experimental half (transferred to oxygen). The actual value obtained in the control group not transferred to oxygen was higher than expected as compared to comparable exposures in air at this intensity, however, and may indicate that the replacement of air by nitrogen in the buds alone is not sufficient, but that it is necessary to make the exposure in an atmosphere devoid of oxygen as well. This problem is being investigated further.

Summary.—Experiments have been performed which indicate that oxygen has a marked effect in increasing the radiosensitivity of Tradescantia chromosomes. Comparative exposures of inflorescences to x-rays were made in air, in nitrogen and in oxygen. A cytological analysis was then made of chromosomal rearrangements (interchanges and interstitial deletions) in microspores at the four- to five-day interval following irradiation. The frequency of aberrations was strikingly reduced when nitrogen replaced air and increased when oxygen replaced air. The magnitude of this effect is very great, the increase in aberration frequency in exposures made in oxygen as compared with nitrogen being as much as fivefold at higher doses. Aberration frequencies were also reduced in additional exposures made in other gases such as helium and argon, demonstrating that the availability of oxygen is a very important factor in the production of chromosomal rearrangements by x-rays. It is not possible on the present evidence to decide whether this effect of oxygen is exerted on the initial breakage mechanism or on the recovery process.

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† On leave from the University of Kentucky.

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[7] The authors would like to express their appreciation to Dr. W. A. Arnold of this laboratory for making these calculations.

THE INFLUENCE OF THE Y-CHROMOSOME ON X-RAY INDUCED MUTATION RATE IN DROSOPHILA MELANOGASTER

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Introduction.—There is an increasing interest in the rôle played by heterochromatin in the synthesis of cellular proteins.[1] Heitz coined the term "heterochromatin" in 1928, and later[2] postulated from purely cytological evidence that heterochromatin would probably prove to be genetically inert. Subsequent work has borne out the essential correctness of this hypothesis. Although practically devoid of genes, heterochromatin, nevertheless, is not inactive.

There are several lines of evidence which indicate that heterochromatin plays a rôle in cellular metabolism. (1) Excessive amounts of heterochromatin may cause sterility, as in the case of the *XYYY* male of *Drosophila melanogaster*.[3] (2) The amount of heterochromatin in the nucleus influences the amount of cytoplasmic nucleic acid. Caspersson and Schultz[4] found that *XXY* ovaries of *D. melanogaster* are richer in cytoplasmic nucleic acid than *XX* ovaries. (3) Heterochromatin causes instability in certain genes upon their transposition from normal euchromatic sites to ones located in or near heterochromatin.[5] Paradoxically, some of these unstable genes are rendered more stable by the addition of extra heterochromatin in the form of supernumerary *Y*-chromosomes.[6] (4) The *Y*-chromosome of Drosophila is instrumental in increasing mutation rate. According to recent work of Mampell[7, 8] there are two actions of the *Y*: first, in *D. pseudoobscura* the *Y*-chromosome is necessary for the activity of the "mutator" gene, a recessive factor, located on chromosome 2, which causes increased mutability; second, the *Y*-chromosome of one species can apparently cause an increased mutability in flies of another species.

It is of interest, therefore, to determine the effect of heterochromatin on x-ray induced mutation frequency. The experiments described here were designed to test the effect of an extra *Y*-chromosome on x-ray induced visible and sex-linked recessive lethal mutation frequency in *D. melanogaster*.

Materials and Methods.—The stock used, No. 766 Stock from the Lankenau Hospital Research Institute,[9] is one in which the *X*-chromosome carries the white-mottled-4 (w^{m4}) inversion (breaks to the left of white, at band 3*C*2, and to the right of band 20, the bobbed locus), and in which the autosomes are from the Oregon-*R* wild stock.

The w^{m4} mutant type, first described by Muller,[10] is considered one of the "eversporting" displacements. Presumably the normal allele of white,

upon its transposition (by means of the w^{m4} inversion) to heterochromatin, becomes unstable and mutates somatically in the developing eye disc to the recessive allele, thereby producing the characteristic mottled phenotype. An extra Y-chromosome increases the stability of w^{m4} and the phenotype becomes more nearly normal.

In the experiments described here, use was made of this effect of an extra Y-chromosome. Phenotypically distinguishable XY and XYY males from the w^{m4} stock were x-rayed simultaneously and their progeny examined for induced visible (attached-X method)[11] and sex-linked recessive lethal (*ClB* method)[12] mutations. Phenotypically distinguishable XX and XXY females from the same stock were also irradiated simultaneously and their progeny examined for visibles.[11]

In conducting the experiments on x-rayed males, the treated flies were bred singly (pair matings) and the males removed after three days to insure testing of only those sperm which were mature at the time of treatment. In the case of irradiated females, the treated flies were bred singly (pair matings) to males, from the attached-X stock, which carried the sex-linked recessive *fu*^{g}; eggs were collected over a ten-day period. For both the male and female series, parallel unirradiated cultures were run as controls.

In the experiments on irradiated males, only certain types of sperm were studied. The XY males from the w^{m4} stock form X- and Y-bearing sperm in the expected ratio of 1:1. The XYY males form four kinds of sperm, XY-, Y-, YY- and X-bearing in the ratio of approximately 7:7:1:1 (this ratio indicates preferential synapsis of the two Y-chromosomes at meiosis: YY synapsis in approximately 76% of spermatocytes and XY synapsis in 24%). The *ClB* method, which was employed for detecting sex-linked recessive lethals, tests only X-bearing sperm from XY males and X- and XY-bearing sperm from XYY males. In these tests for induced lethals in sperm, it was not possible with the *ClB* stock employed to distinguish between X- and XY-bearing sperm of the XYY males. With the attached-X method for visibles, however, such a distinction could be made. In the data presented below, where the total visible rate was measured, both types of sperm from XY males and all four types from XYY males are included.

The XXY females from the w^{m4} stock form four kinds of eggs: XY, X, XX and Y, in the approximate ratio of 9:9:1:1. In the irradiation studies on the XXY females, XY, X and XX eggs were scored.

Results.—On the basis of the experiments performed, three types of comparison can be made: first, a comparison of the frequency of visible mutations induced in the X- and XY-bearing sperm of XYY males and in the X-bearing sperm of both XY and XYY males; second, a comparison of the relative frequencies of visible mutations in the progeny of irradiated XX and XXY females; third, a comparison of the relative frequencies

of total visible and sex-linked recessive lethal mutations in the progeny of irradiated XY and XYY males.

In terms of the actual data, these three comparisons are as follows: (1) The XY sperm of treated XYY males show a lower visible mutation rate than X-bearing sperm from the same males (22 mutants[13] in 2974 flies, or 0.74% as opposed to 9 mutants in 521 flies, or 1.73%; the exact P value of this difference, as determined by chi square, is 0.062—see table

TABLE 1

VISIBLE MUTATIONS SCORED ACCORDING TO TYPE OF SPERM

	TOTAL FLIES	NO. OF MUTANTS	MUTATION RATE, %	P VALUE OF DIFFERENCE
	Irradiated[21] (*4000 r*)			
X sperm from XY males	1452	36	2.47	
				0.434
X sperm from XYY males	521	9	1.73	
				0.062
XY sperm from XYY males	2974	22	0.74	
	Control (*Untreated*)			
X sperm from XY males	1176	4	0.34	
				0.962
X sperm from XYY males	243	0	0.00	
				0.77
XY sperm from XYY males	1758	2	0.11	

TABLE 2

VISIBLE MUTATION FREQUENCY IN FEMALES

	NO. OF CULTURES	TOTAL FLIES	FLIES PER CULTURE	NO. OF MUTANTS	MUTATION RATE, %	P VALUE DIFFERENCE
		Irradiated (*2000 r*)				
XX females	123	2615	21.2	12	0.46	
						0.996
XXY females	270	4679	17.3	23	0.49	
		Control (*Untreated*)				
XX females	41	1660	40.5	0	0.00	
XXY females	42	1325	31.5	0	0.00	

1). The X-bearing sperm from the two kinds of males show mutation rates which are not significantly different (36 mutants in 1452 flies, or 2.47%, and 9 mutants in 521 flies, or 1.73%; the P value of this difference is 0.434—see table 1). (2) There is no significant difference in the visible mutation rates in x-rayed XXY and XX females (23 mutants in 4679 flies, or 0.49%, as opposed to 12 mutants in 2615 flies, or 0.46%; the P value of this difference is 0.996—see table 2). (3) The total visible mutation rate for irradiated XYY males is significantly lower than that for

XY males (32 mutants in 6498 flies, or 0.49%, as opposed to 37 mutants in 3151 flies, or 1.17%, the difference having a P value of 0.0005—see table 3). And, in the case of the sex-linked recessive lethals,[14] where the observations are completely objective, the mutation rate obtained for the XYY males is much lower than the rate obtained for XY males (22 cultures out of a total of 344 showed lethals, giving a rate of 6.40%, as opposed to 35 cultures out of a total of 286, giving a rate of 12.24%; the P value of the difference is 0.014—see table 4).

Discussion.—In connection with the experiments presented here, there are three points which bear discussion.

TABLE 3

VISIBLE MUTATION FREQUENCY IN MALES

	NO. OF CULTURES	TOTAL FLIES	FLIES PER CULTURE	NO. OF MUTANTS	MUTATION RATE, %	P VALUE DIFFERENCE
			Irradiated (4000 r)			
XY males	421	3151	7.48	37	1.17	
						0.0005
XYY males	655	6498	9.77	32	0.49	
			Control (Untreated)			
XY males	48	2180	45.4	3	0.14	
						0.065
XYY males	61	3145	51.6	2	0.064	

TABLE 4

RECESSIVE SEX-LINKED LETHAL MUTATION FREQUENCY IN MALES

	TOTAL F_2 CULTURES	NO. OF CULTURES WITH LETHAL	MUTATION RATE, %	P VALUE OF DIFFERENCE
		Irradiated (4000 r)		
XY males	286	35	12.24	
				0.014
XYY males	344	22	6.40	
		Control (Untreated)		
XY males	347	2	0.58	
				0.085
XYY males	189	2	1.06	

In the first place, it is demonstrated that an extra Y-chromosome, when present in the male, significantly decreases both the visible and sex-linked lethal mutation rates. Moreover, there are two lines of evidence which indicate that the influence of the extra Y is not exerted until after meiosis: (1) the visible mutation rate induced in X-bearing sperm of XY males is not significantly different from the rate induced in X-bearing sperm of XYY males; (2) XY-bearing sperm from XYY males show a lower frequency of induced visibles than X-bearing sperm from the same males. It is not possible in the sex-linked recessive lethal series to determine

whether the action of the extra Y precedes or follows meiosis, since the X- and XY-bearing sperm of the XYY males are indistinguishable.

Second, the exact mode of action of the extra Y in the sperm is not understood. The extra heterochromatin may shield the chromosomes from the ionizing effects of the x-rays, or it may provide a reservoir of material for chromosome restitution, thereby decreasing the frequency of chromosomal rearrangements and consequently decreasing the frequency of position effects. If the latter were true, the lack of effect of the Y in treated females might be understandable, since interchromosomal rearrangements are known to occur at a negligible rate in irradiated eggs.[15-17] Recent preliminary studies of Dr. H. B. Glass seem to indicate that the frequency of reciprocal translocations induced by x-rays in Drosophila eggs can be increased if the females are exposed to infra-red following x-ray treatment (personal communication). This work suggests a type of experiment which may throw light on the mode of action of the Y-chromosome in the present experiments. If an extra Y decreases the frequency of interchromosomal exchange, infra-red post-treatment of irradiated females should provide experimental conditions favorable for the detection of such action. Additional experiments which may help to throw light on the failure of the Y action in females are planned. They will involve a comparative study on sex-linked recessive lethal mutations induced in XX and XXY females.

Finally, if the extra Y chromosome retards maturation so that there are more immature germ cells in XYY testes than in XY testes, this might conceivably account for the lowered mutation rate.[18-20] Experiments to test this possibility are already under way.

Summary.—The results of experiments described here show that an extra Y-chromosome, when present in the male of *Drosophila melanogaster*, decreases x-ray induced visible and sex-linked lethal mutation frequency. In the female, an extra Y appears to be without effect. The possible mode of action of the Y has been discussed and future lines of investigation proposed.

* This work was done during the tenure of Predoctorate Fellowships from the Donner Foundation and from the U. S. Public Health Service (National Cancer Institute).

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[2] Heitz, E., *Planta. Archiv für wissenschaftliche Botanik. Abteilung E der Zeitschrift für Biologie*, **18**, 571–636 (1932).

[3] Schultz, J., *Proc. VIIth Int. Genet. Cong., Edinburgh*, pp. 257–262 (1941).

[4] Caspersson, T., and Schultz, J., *Nature*, **142**, 294–295 (1938).

[5] Demerec, M., *Genetics*, **25**, 618–627 (1940).

[6] Gowen, J. W., and Gay, E. H., these PROCEEDINGS, **19**, 122–126 (1933).

[7] Mampell, K., *Genetics*, **30**, 498–505 (1945).

[8] Mampell, K., *Ibid.*, **31**, 589–597 (1946).

[9] The author is indebted to Dr. Jack Schultz for this stock.

[10] Muller, H. J., *J. Genet.*, **22**, 299–334 (1930).

[11] No attempt was made to detect autosomal recessives.

[12] The F_2 progenies derived from XYY males and $C1B$ females were examined microscopically in order to eliminate the possibility that patroclinous sons resulting from secondary non-disjunction might mask a lethal.

[13] Breeding tests were conducted on all flies showing conspicuous, symmetrical alterations in phenotype, and such changes were scored as mutants even in those cases where inviability or sterility prevented actual progeny counts.

[14] It should be noted that it was not possible to compare the recessive lethal rates in the two kinds of sperm (X and XY) from XYY males, as was possible in the case of visibles.

[15] Glass, H. B., *Genetics*, **25**, 117 (1940).

[16] Metz, C. W., and Bozeman, M. L., *Carnegie Inst. Wash. Year Book*, **41**, 237–242 (1942).

[17] Reynolds, J. P., these PROCEEDINGS, **27**, 204–208 (1941).

[18] Harris, B. B., *J. Hered.*, **20**, 299–302 (1929).

[19] Kossikov, K. V., *Genetics*, **22**, 213–224 (1937).

[20] Cooper, K. W., *J. Morph.*, **84**, 81–121 (1949).

[21] X-raying was done at the University of Pennsylvania Hospital, through the courtesy of the Department of Radiology. A medium-voltage therapy machine was used with no filter; target distance, 17 cm.; average output, 450 r per minute; current maintained at 8 milliamperes and 135 kilovolts.

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*ON A THEOREM OF WEYL CONCERNING EIGENVALUES OF LINEAR TRANSFORMATIONS. I**

BY KY FAN

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Communicated by Hermann Weyl, September 22, 1949

H. Weyl[1] recently proved the following theorem:

THEOREM. *Let A be a linear transformation in the n-dimensional unitary space C_n. Let the eigenvalues of A and A^*A be denoted by λ_i and $\kappa_i (1 \leq i \leq n)$, respectively, which are so arranged that*

$$|\lambda_1| \geq |\lambda_2| \geq \ldots \geq |\lambda_n|, \qquad \kappa_1 \geq \kappa_2 \geq \ldots \geq \kappa_n. \tag{1}$$

For any non-decreasing function $\omega(t)$ on $t > 0$ such that $\omega(e^t)$ is a convex function of t and $\omega(0) = \lim_{t \to 0} \omega(t) = 0$, λ_i and κ_i satisfy the inequalities:

$$\sum_{i=1}^{q} \omega(|\lambda_i|^2) \leq \sum_{i=1}^{q} \omega(\kappa_i) \qquad (1 \leq q \leq n). \tag{2}$$

In the present note, we prove three related theorems. Theorem 1 gives an extremum property of the sum of the first q eigenvalues for Hermitian transformations. This property furnishes a recurrent charac-

terization of successive eigenvalues without referring to any eigenvector. Theorem 2 gives a similar but stronger property for all normal transformations. For an arbitrary linear transformation A and for a positive integer s, we have in Theorem 3 inequalities comparing the eigenvalues of $(A^s)^*A^s$ with those of A^*A. Finally we shall see that Weyl's theorem in the most important case $\omega(t) = t^s$ ($s = 1, 2, 3, \ldots$) can be derived from Theorems 1 and 3. The general case of Weyl's theorem will be discussed in a forthcoming note.[2] All linear transformations considered here are assumed to be in the n-dimensional unitary space C_n, but the results can be easily carried over to completely continuous linear operators in Hilbert space, especially to continuous kernels of linear integral equations.

THEOREM 1. *Let the eigenvalues λ_i of a Hermitian transformation H be so arranged that $\lambda_1 \geq \lambda_2 \geq \ldots \geq \lambda_n$. For any positive integer $q \leq n$, the sums $\sum_{i=1}^{q} \lambda_i$ and $\sum_{i=1}^{q} \lambda_{n+1-i}$ are, respectively, the maximum and minimum of $\sum_{j=1}^{q} (Hx_j, x_j)$, when q orthonormal vectors x_j ($1 \leq j \leq q$) vary in the space.*[3]

Proof: Let $\varphi_i (1 \leq i \leq n)$ be an orthonormal set of eigenvectors of H: $H\varphi_i = \lambda_i\varphi_i$. For each j, we write

$$(Hx_j, x_j) = \lambda_q \sum_{i=1}^{n} |(x_j, \varphi_i)|^2 + \sum_{i=1}^{q} (\lambda_i - \lambda_q) |(x_j, \varphi_i)|^2 + \sum_{i=q+1}^{n} (\lambda_i - \lambda_q) |(x_j, \varphi_i)|^2. \quad (3)$$

If $\|x_j\| = 1$, then

$$(Hx_j, x_j) \leq \lambda_q + \sum_{i=1}^{q} (\lambda_i - \lambda_q) |(x_j, \varphi_i)|^2$$

and therefore

$$\sum_{i=1}^{q} \lambda_i - \sum_{j=1}^{q} (Hx_j, x_j) \geq \sum_{i=1}^{q} (\lambda_i - \lambda_q) \{1 - \sum_{j=1}^{q} |(x_j, \varphi_i)|^2\}. \quad (4)$$

If x_j ($1 \leq j \leq q$) are orthonormal, then $\sum_{j=1}^{q} |(x_j, \varphi_i)|^2 \leq \|\varphi_i\|^2 = 1$, so that the right-hand side of (4) is ≥ 0. But the left-hand side vanishes for $x_j = \varphi_j$ ($1 \leq j \leq q$). This proves the maximum property.

THEOREM 2. *Let λ_i be the eigenvalues of a normal transformation N so arranged that $|\lambda_1| \geq |\lambda_2| \geq \ldots \geq |\lambda_n|$. Let s, q be two positive integers ($q \leq n$). Then $\sum_{i=1}^{q} |\lambda_i|^{2s}$ is the maximum of $\sum_{j=1}^{q} \|(UN)^s x_j\|^2$, when U runs over all unitary transformations and x_j ($1 \leq j \leq q$) runs over all sets of q orthonormal vectors in C_n.*

Proof: We need only prove the inequality

$$\sum_{j=1}^{q} \|(UN)^s x_j\|^2 \leq \sum_{i=1}^{q} |\lambda_i|^{2s}. \tag{5}$$

As $\|UNx_j\|^2 = (N^*Nx_j, x_j)$, the case $s = 1$ of (5) follows from Theorem 1. We proceed by induction, assuming that (5) is true for s. Let $\varphi_i (1 \leq i \leq n)$ be an orthonormal set of eigenvectors of N: $N\varphi_i = \lambda_i \varphi_i$. Consider a unitary transformation U and q orthonormal vectors x_j $(1 \leq j \leq q)$. We have $\|(UN)^{s+1}x_j\|^2 = \sum_{i=1}^{n} |\lambda_i|^2 \cdot |((UN)^s x_j, \varphi_i)|^2$. If we split this sum into three parts in a way similar to (3), we see that for each j:

$$\|(UN)^{s+1}x_j\|^2 \leq |\lambda_q|^2 \cdot \|(UN)^s x_j\|^2 + \sum_{i=1}^{q} (|\lambda_i|^2 - |\lambda_q|^2) \cdot |((UN)^s x_j, \varphi_i)|^2. \tag{6}$$

As $x_j (1 \leq j \leq q)$ are orthonormal, we have for each i:

$$\sum_{j=1}^{q} |((UN)^s x_j, \varphi_i)|^2 \leq \|(N^*U^*)^s \varphi_i\|^2 = \|(U^*N^*)^s U^* \varphi_i\|^2. \tag{7}$$

Using first (6), then (7) and our assumption of induction (i.e. (5) is true for s), we get

$$\sum_{i=1}^{q} |\lambda_i|^{2s+2} - \sum_{j=1}^{q} \|(UN)^{s+1}x_j\|^2 \geq \sum_{i=1}^{q} (|\lambda_i|^2 - |\lambda_q|^2)[|\lambda_i|^{2s} - \|(U^*N^*)^s U^* \varphi_i\|^2]. \tag{8}$$

Denote by d_q the expression on the right-hand side of (8), we have

$$d_{q+1} - d_q = (|\lambda_q|^2 - |\lambda_{q+1}|^2)[\sum_{i=1}^{q} |\lambda_i|^{2s} - \sum_{i=1}^{q} \|(U^*N^*)^s U^* \varphi_i\|^2]. \tag{9}$$

As $U^*\varphi_i (1 \leq i \leq q)$ are orthonormal, our assumption of induction shows that the right-hand side of (9) is ≥ 0, and $d_{q+1} \geq d_q$. But $d_1 = 0$, hence $d_q \geq 0$. This proves that (5) is also true for $s + 1$.

THEOREM 3. *Let A be an arbitrary linear transformation and s be any positive integer. Let the eigenvalues of $(A^s)^*A^s$ be denoted by $\kappa_i^{(s)} = \kappa_i$) and so arranged that $\kappa_1^{(s)} \geq \kappa_2^{(s)} \geq \ldots \geq \kappa_n^{(s)}$. Then for any positive integer $q \leq n$, we have*

$$\sum_{i=1}^{q} \kappa_i^{(s)} \leq \sum_{i=1}^{q} \kappa_i^s. \tag{10}$$

Proof: Let $A = UH$ be the polar decomposition of A, where U is unitary and H is the non-negative square root of A^*A. The eigenvalues of

H are $\kappa_i^{1/s}$. By Theorem 2, any q orthonormal vectors $x_j (1 \leq j \leq q)$ satisfy

$$\sum_{j=1}^{q} ((A^s)^* A^s x_j, x_j) = \sum_{j=1}^{q} \|(UH)^s x_j\|^2 \leq \sum_{i=1}^{q} \kappa_i^s. \tag{11}$$

But by Theorem 1, $\sum_{i=1}^{q} \kappa_i^{(s)}$ is the maximum of the first $\sum$ sum in (11), when the q orthonormal vectors x_j vary. Thus (10) is proved.

We now prove the case $\omega(t) = t^s (s = 1, 2, 3, \ldots)$ of Weyl's theorem. Here we use the same notation as in the theorem stated at the beginning of this note. Using Schur's superdiagonal form of matrices, it is clear that there exist n orthonormal vectors $y_i (1 \leq i \leq n)$ such that $|\lambda_i|^2 \leq \|Ay_i\|^2 (1 \leq i \leq n)$ and therefore $\sum_{i=1}^{q} |\lambda_i|^2 \leq \sum_{i=1}^{q} \|Ay_i\|^2$. But applying Theorem 1 to A^*A, we find $\sum_{i=1}^{q} \|Ay_i\|^2 \leq \sum_{i=1}^{q} \kappa_i$. Hence

$$\sum_{i=1}^{q} |\lambda_i|^2 \leq \sum_{i=1}^{q} \kappa_i. \tag{12}$$

As in Theorem 3, we denote by $\kappa_i^{(s)}$ the eigenvalues of $(A^s)^* A^s$ arranged in descending order (in particular, $\kappa_i^{(1)} = \kappa_i$). Applying (12) to the transformation A^s, we get

$$\sum_{i=1}^{q} |\lambda_i|^{2s} \leq \sum_{i=1}^{q} \kappa_i^{(s)},$$

which together with (10) gives the case $\omega(t) = t^s$ of (2).

* This work was supported in part by the Office of Naval Research.

[1] Weyl, H., "Inequalities between the Two Kinds of Eigenvalues of a Linear Transformation," these PROCEEDINGS, **35**, 408–411 (1949).

[2] Fan, K., "On a Theorem of Weyl concerning Eigenvalues of Linear Transformations. II," to be published in these PROCEEDINGS.

[3] An alternative form of Theorem 1: $\sum_{i=1}^{q} \lambda_i$ and $\sum_{i=1}^{q} \lambda_{n+1-i}$ are, respectively, the maximum and minimum of the trace of HP, when P runs over all projections on q-dimensional linear subspaces. There is also a similar alternative form of Theorem 2.

ON SELF-ADJOINT DIFFERENTIAL EQUATIONS OF SECOND ORDER

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This note is an abstract of a longer paper which will be published elsewhere.

The paper is concerned with the behavior near $x = +\infty$ of solutions of the self-adjoint differential equation

$$(r(x)y')' + p(x)y = 0, \tag{1}$$

where $r(x) > 0$ and $r(x)$, $r'(x)$ and $p(x)$ are continuous functions of the real variable x for $x > 0$. The theorem which follows enables one to compare the rapidity of oscillation of a solution of (1) with that of a solution of

$$(r(x)z')' + p_1(x)z = 0. \tag{2}$$

THEOREM 1. *If for all solutions $y(x)$ and $z(x)$ of (1) and (2), respectively, the function*

$$W(x) = r(x)[y(x)z'(x) - y'(x)z(x)]$$

either is eventually of fixed sign or has the limit zero as x becomes infinite, the zeros of some solution $y(x)$ eventually separate those of each non null solution $z(x)$, and vice versa.

COROLLARY. *If all solutions $y(x)$ and $z(x)$ are bounded and if the limit*

$$\lim_{x \to \infty} \int_a^x |p - p_1| \, dx$$

exists (in the strict sense), the conclusion of Theorem 1 is valid.

The results stated are valid whether or not the solutions of (1) and of (2) are oscillatory near $x = \infty$.

In studying (1) it is frequently useful to write linearly independent solutions of this equation in the *canonical* form

$$u(x) \sin v(x), \qquad u(x) \cos v(x) \tag{3}$$

used by Milne, Fatou and others. Here $u(x)$ and $v(x)$ may be assumed to be positive for $x > 0$. A companion theorem of an earlier result[1] is this.

THEOREM 2. *If $p(x) > 0$ and $p(x)r(x)$ is monotone decreasing as x increases, there exists a positive constant c^2 such that $u(x) \geq c^2$ for $x \geq a > 0$.*

If $r = 1$, and $p(x) > 0$ and of class C^2, write $p(x) = [q(x)]^{-4}$. The following theorem may then be stated.

THEOREM 3. *Suppose $Q = (1 + q^3q'')$ is positive for x large. If Q is monotone increasing as x increases, each solution $y(x)$ of (1) has the property*

that $|y(x)| \leq Mq(x)$, *where* M *is a positive constant. If* Q *decreases monotonely as* x *increases, corresponding to each solution* $y(x)$ *there exists a positive constant* m *such that*

$$u(x) \geq mq(x),$$

where $u(x)$ *is any coefficient in* (3).

A number of necessary conditions that solutions of (1) be oscillatory (i.e., sufficient conditions for non-oscillation) near $x = \infty$ are given. A principal theorem is the following.

THEOREM 4. *If* $r = 1$ *and* $x^2p(x) - 1/4$ *is a positive monotone function of* x, *a necessary condition that a solution* $y(x)$ *of* (1) *be oscillatory near* $x = \infty$ *is that*

$$\lim_{x \to \infty} \int_1^x [(x^2p(x) - 1/4)^{1/2}/x]dx = \infty.$$

A number of corollaries may be stated. The following is of interest as a companion result to an earlier one given by the present author.[2]

COROLLARY. *If* $p(x)r(x)$ *is a positive monotone function of* x *for* x *large, a necessary condition that solutions* $y(x)$ *of* (1) *be oscillatory neighboring* $x = \infty$ *is that not both limits*

$$\lim_{x \to \infty} \int_1^x \frac{dx}{r(x)}, \qquad \lim_{x \to \infty} \int_1^x p(x)dx$$

exist.

Proofs of the theorems stated and of other related results, as well as a more complete bibliography, will be given in the longer paper of which this is an abstract.

[1] These PROCEEDINGS, **35**, 190 (1949).

[2] *Ibid.*, **35**, 193 (1949).

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*THE COEFFICIENT PROBLEM FOR BOUNDED SCHLICHT FUNCTIONS**

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Communicated by S. Lefschetz, September 9, 1949

The theory of the class of bounded schlicht functions is in some respects more symmetric than that of the general class of schlicht functions, and it is the purpose of the present paper to give some of the preliminary theory and to indicate some of the problems attached to this class of functions.

1. Consider the two classes of functions: the class S, consisting of all functions of the form

$$w = f(z) = z + a_2z^2 + a_3z^3 + \ldots$$

which are regular and schlicht in $|z| < 1$; the class $\mathfrak{B}S$, consisting of all functions of the form

$$w = f(z) = b_1z + b_2z^2 + b_3z^3 + \ldots$$

with $b_1 > 0$, which are regular, schlicht and bounded by unity in $|z| < 1$. The set of all the points $(a_2, \ldots, a_n)$ which belong to functions of class S form, in $(2n - 2)$-dimensional space, the closed domain V_n, which has been studied by Schaeffer and Spencer.[6] Similarly, the set of all points $(b_1, b_2, \ldots, b_n)$ belonging to functions of class $\mathfrak{B}S$ form a region $\mathfrak{V}_n$ in $(2n - 1)$-dimensional space. Each bounded function of class S is transformed into a function of $\mathfrak{B}S$ on division by its maximum modulus, and each function of $\mathfrak{B}S$ is transformed into a bounded function of S on division by b_1.

Since the class $\mathfrak{B}S$ becomes compact with the addition of the function $w = 0$, the region $\mathfrak{V}_n + 0$ (the origin) is closed. It can be shown that a necessary and sufficient condition that the point $(b_1, b_2, \ldots, b_n)$ be an interior point of $\mathfrak{V}_n$ is the existence of a function $f(z) \in \mathfrak{B}S$ belonging to the point and bounded by $r < 1$ in $|z| < 1$. Hence $\mathfrak{V}_n + 0$ is the closure of its interior.

Each interior point $(a_2, \ldots, a_n)$ of V_n determines a segment $(b_1, b_1a_2, \ldots, b_1a_n)$ of $\mathfrak{V}_n$ as b_1 varies from 0 to b_1^*, the maximum value b_1 can have for the point $(b_1, b_1a_2, \ldots, b_1a_n)$ to belong to $\mathfrak{V}_n$. The end points can be the only points of intersection with the boundary of $\mathfrak{V}_n + 0$, since all the other points are interior points. Now b_1^* will be the reciprocal of the minimum of the maximum moduli of the functions of class S belonging to the point $(a_2, \ldots, a_n)$. We have $b_1^* > 0$, since the interior points of V_n possess bounded functions.[6]

To construct $\mathfrak{V}_n$ starting from V_n, one first constructs a cone in $(2n - 1)$-dimensional space with vertex at the origin and base V_n in the hyperplane $b_1 = 1$. Cut each ray from the origin to an interior point of V_n off at a vertical distance b_1^* from the origin. The segments from the origin to $(b_1^*, b_1^*a_2, \ldots, b_1^*a_n)$ form $\mathfrak{V}_n$.

It now follows that b_1^* is a continuous function of the point $(a_2, \ldots, a_n)$, for if b_1^* had more than one limit point as we approach the point $(a_2, \ldots, a_n)$ we would have more than one boundary point of $\mathfrak{V}_n$ on the segment $(b_1, b_1a_2, \ldots, b_1a_n)$, $0 < b_1 \leqslant b_1^*$, which is impossible. From this follows the continuity of the minimum of the maximum moduli of the functions of S belonging to interior points of V_n.

Since V_n is topologically equivalent to the closed $(2n - 2)$-dimensional

sphere, $\mathfrak{V}_n + 0$ is equivalent to the closed $(2n - 1)$-dimensional sphere.

2. Let the continuous, real valued function F have a continuous and non-vanishing gradient in an open set containing $\mathfrak{V}_n + 0$. Then on the basis of the formula (2.5.2) of reference 6, one has the following lemma, which has also been obtained by Charzyński.[2]

LEMMA: *Every function $w = f(z)$ of class $\mathfrak{B}S$ belonging to a point $(b_1, b_2, \ldots, b_n)$ where F attains its maximum in $\mathfrak{V}_n$ must satisfy the differential equation*

$$\left(\frac{z}{w}\frac{dw}{dz}\right)^2 R(w) = Q(z) \tag{1}$$

where

$$R(w) = \sum_{\nu=-n+1}^{n-1} \frac{\beta_\nu}{w^\nu}, \quad Q(z) = \sum_{\nu=-n+1}^{n-1} \frac{B_\nu}{z^\nu}. \tag{2}$$

Moreover, the functions $R(w)$ and $Q(z)$ are real and non-negative on the unit circumference, and each has at least one zero there. If we set $F_k = \dfrac{\partial F}{\partial b_k}$, then

$$\begin{aligned} \beta_\nu &= \sum_{k=\nu+1}^{n} F_k b_k^{(\nu+1)}, & \beta_{-\nu} &= \bar{\beta}_\nu \\ & & \beta_0 &= {}^1/_2 F_1 b_1 + Re \sum_{k=2}^{n} b_k F_k \\ B_\nu &= \sum_{k=1}^{n-\nu} k b_k F_{k+\nu}, & B_{-\nu} &= \bar{B}_\nu \\ & & B_0 &= {}^1/_2 F_1 b_1 + Re \sum_{k=2}^{n} k b_k F_k. \end{aligned} \tag{3}$$

Thus it is clear that an equation of the form (1) is satisfied by the functions belonging to a dense set of boundary points, and by a limiting process such an equation is seen to be satisfied at every boundary point (except of course at $(0, \ldots, 0)$), where now the F_k are merely certain constants. Such equations will be called $\mathfrak{D}_n$-equations, provided that if k is the largest integer such that $B_k \neq 0$, then $b_1^k \beta_k = B_k$ and all $\beta\nu = 0$ for $\nu > k$. This last condition is obviously necessary for the existence of solutions analytic at $z = 0$. A function $w = f(z)$ which is regular in $|z| < 1$ and which has a positive derivative at the origin will be called a $\mathfrak{D}_n$-function if it satisfies a $\mathfrak{D}_n$-equation. We must have $b_1 < 1$ for $f(z)$ to be bounded by unity, but this is the only restriction to be placed on b_1.

If $\zeta = \int \sqrt{Q(z)}\, dz/z$, we let Γ_z be the set of arcs $Re(\zeta) =$ constant which have one or both end-points at a zero of $Q(z)$. This Γ_z-structure has been investigated in [6]. The Γ_w-structure is similarly defined in connection with $R(w)$, and in our case it has exactly the same form as the Γ_z-structure. Using methods similar to those in reference 6, the following theorem can be established.

THEOREM I: *If $w = f(z)$ is a $\mathfrak{D}_n$-function, then it is schlicht in $|z| < 1$ and maps $|z| < 1$ onto the interior of the unit circle minus a subcontinuum of Γ_w containing the circle $|w| = 1$. By continuation from within $|z| < 1$ the function $f(z)$ is regular on $|z| = 1$ with the exception of finitely many points where it has the local development*

$$f(z) = \sum_{\nu=0}^{\infty} \alpha_\nu (z - e^{i\varphi})^{\nu/m},$$

m a positive integer.

Let C_w be a subcontinuum of Γ_w interior to and containing the circle $|w| = 1$. Let

$$\psi(w) = w + \alpha w^n + \beta w^{n+1} + \ldots$$

be regular, schlicht and bounded by unity in the complement of C_w in $|w| < 1$. Then, using the method of Teichmüller,[7] we can show that $Re(\alpha\beta_{n-1}) \leqslant 0$, with equality if and only if $\psi(w) = w$. From this follows Theorem II.

THEOREM II: *Every $\mathfrak{D}_n$-function belongs to some boundary point of $\mathfrak{V}_n$, and to any given boundary point of $\mathfrak{V}_n$ (except $(0, 0, \ldots, 0)$) there belongs one and only one $\mathfrak{D}_n$-function.*

THEOREM III: *Of all the functions of class S which belong to the interior point $(a_2, \ldots, a_n)$ of V_n, the one which has the smallest maximum modulus is unique and is $1/b_1^*$ times the $\mathfrak{D}_n$-function belonging to the point $(b_1^*, b_1^* a_2, \ldots, b_1^* a_n)$ of the boundary of $\mathfrak{V}_n$.*

This is a modification of a problem considered by Carathéodory and Fejer,[1] who did not require their functions to be schlicht.

3. If a part of the boundary of $\mathfrak{V}_n$ is smooth, then we can choose the function F of our lemma in such a manner that it vanishes on any given open subset S of this part of the boundary and is non-positive on the remainder of the boundary. Then by the lemma equation (1) is satisfied at each point of S by the function belonging to this point. Hence at each point of S there is a complex number $\bar{\kappa}$ of unit modulus such that

$$Q(\bar{\kappa}) = 0, \qquad Q'(\bar{\kappa}) = 0. \tag{4}$$

If we assume $B_{n-1} \neq 0$, a necessary and sufficient condition for the existence of a $\bar{\kappa}$ satisfying equations (4) is the vanishing of their resultant. The B_ν are given by (3), where the $F\nu$ now determine the normal direction to the boundary of $\mathfrak{V}_n$. Thus the resultant becomes a non-linear first order partial differential equation for S.

If we consider the second of equations (4) as determining $\bar{\kappa}(B_\nu, \bar{B}_\nu)$, then the resultant is equivalent to

$$2Q(\bar{\kappa}) = 0. \tag{5}$$

The characteristics of (5) are given by[8]

$$\frac{db_k}{dt} = 2\frac{\partial Q(\kappa)}{\partial F_k} = 2\sum_{\nu=-n+1}^{n-1} \kappa^\nu \frac{\partial B}{\partial F_k} + 2Q'(\kappa)\frac{\partial \kappa}{\partial F_k}.$$

Since $Q'(\kappa) = 0$, this results in

$$\frac{db_k}{dt} = kb_k + 2\sum_{\nu=1}^{k-1} (k-\nu) b_{k-\nu}\kappa^\nu. \tag{6}$$

These are the same as the equations obtained by equating coefficients in the differential equation

$$\frac{\partial g(z,t)}{\partial t} = z\frac{\partial g(z,t)}{\partial z}\frac{1+\kappa z}{1-\kappa z}, \tag{7}$$

which was obtained by Löwner[3] and shown to apply to arbitrary slit mappings. In our case the function $g(z, t)$ maps onto the complement of a subcontinuum of a fixed Γ_w-structure. With increasing t the subcontinuum is cut away until a time t_0 when $g(z, t_0) = z$. With decreasing t the subcontinuum grows and $g(z, t) \to 0$ as $t \to -\infty$. Thus the points $(1, 0, \ldots, 0)$ and $(0, 0, \ldots, 0)$ are critical points of the differential equation (5).

Had we started with the function $R(w)$ instead of $Q(z)$ we should have obtained a different equation whose characteristics are

$$\frac{db_k}{d_t} = -(b_k + 2\sum_{\nu=1}^{k-1} \kappa^\nu b_k^{(\nu+1)}).$$

These correspond to the dual Löwner equation

$$\frac{\partial f(z,t)}{\partial t} = -f\frac{1+\kappa f}{1+\kappa f}$$

4. We conclude by giving the form of the body $\mathfrak{V}_2$. Here $Q(z)$ must be of the form $c(e^{i\theta}z^{-1} + 2 + e^{-i\theta}z)$ and $R(w)$ must be $b_1 c(e^{i\theta}w^{-1} + 2 + e^{-i\theta}w)$. Equation (1) becomes

$$b_1^{1/2}(w + e^{i\theta})\frac{dw}{\sqrt{w^3}} = (z + e^{i\theta})\frac{dz}{\sqrt{z^3}}$$

Hence by integration

$$\frac{b_1 z}{(1 - ze^{i\theta})^2} = \frac{w}{(1 - we^{i\theta})^2}. \tag{8}$$

The functions $w = f(z)$ defined by (8) map the unit circle onto the unit circle minus a straight slit orthogonal to the unit circle at $w = -e^{-i\theta}$. Calculating the coefficient of b_2 we get $b_2 = -2(b_1 - b_1^2)e^{-i\theta}$, or $b_2 =$

$2b_1(1 - b_1)$. This is an equation for the boundary of $\mathfrak{V}_2$ and is in accord with the result of Pick.[4]

It is interesting to note that for $n = 2$ the resultant of equations (4) becomes $B_0^2 = 4|B_1|^2$. Writing $b_2 = re^{i\varphi}$, we have

$$b_1^2(F_r^2 + F_\varphi^2) = (\tfrac{1}{2}b_1F_{b_1} + rF_r)^2. \tag{9}$$

Since we can change the argument of b_2 without changing its modulus merely by rotating both the z and w planes, F must be independent of φ. Thus (9) becomes an ordinary differential equation which separates and integrates into

$$-\frac{1}{b_1} + c = -\frac{1}{2}\left(\frac{r}{b_1^2}\right).$$

Since $r = 0$ at $b_1 = 1$, c must be zero giving $r = 2(b_1 - b_1^2)$ as before.

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[8] The characteristics of V_n were first discussed in reference (5).

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